

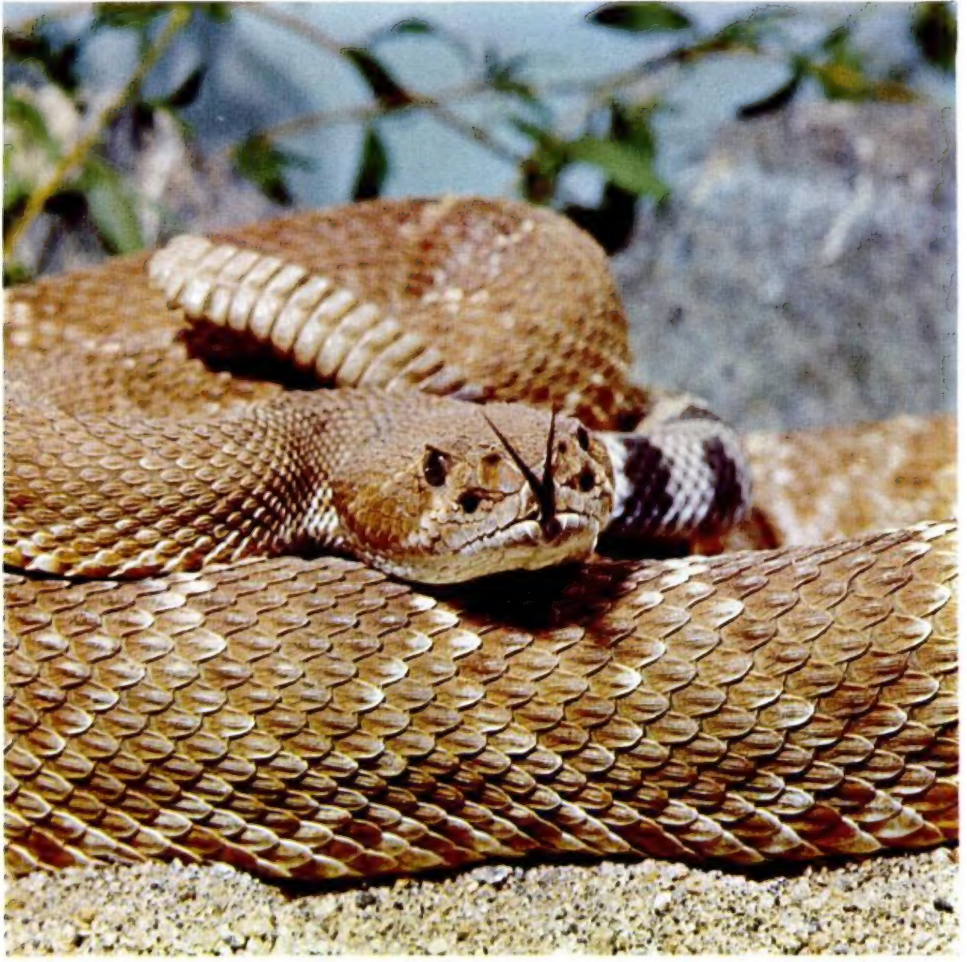
# RATTLESNAKES

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This One



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The Red Diamond Rattlesnake (*Crotalus ruber ruber*) is found in southern California and northern Baja California, Mexico. (San Diego Zoo photo by Ron Garrison.)

# RATTLESNAKES

*Their Habits, Life Histories, and  
Influence on Mankind*

*In Two Volumes ♦ Volume I*

LAURENCE M. KLAUBER

*Second Edition*

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*Designed by Rita Carroll*

# DEDICATION

*To my wife, Grace, who not only  
endured a basement full of rattlesnakes  
for more than thirty years, but also suffered the  
annoying imposition of austerity that  
goes with research in the home*

## Preface to the Second Edition

This edition contains such changes and additions as have been made possible by new knowledge of rattlesnakes obtained by herpetological students and field observers during the intervening years. The new material has been inserted at appropriate places in the text and the references detailing the new information have been added to the bibliography. The extended knowledge has been especially important in the fields of classification. Newly described subspecies have been included and others not hitherto considered valid have been reinstated. The range maps and morphological tables have been brought up to date.

Almost everywhere rattlesnake populations are diminishing because of the influx of people into the rural areas where they are found; but, coincidentally, there are more people who are curious about these interesting, but unfortunately dangerous, reptilian neighbors, thus justifying this republication.

### PUBLISHER'S NOTE

Laurence M. Klauber's monumental study, *Rattlesnakes*, was first published in 1956. The two-volume work was subsequently given the highest critical acclaim and the author became internationally recognized as the outstanding authority on the subject. Over the next several years, Mr. Klauber continued to collect information aimed at the eventual publication of a revised edition. Work on this began in earnest in 1966 and the author completed revisions to chapters 1, 2, and 3 in 1967. He regarded these changes as being the most necessary and significant in the entire work. The revised chapter 2 incorporates all the information available on classification and identification of rattlesnake species and subspecies up to the end of 1967. Chapter 3 has been greatly expanded in the light of recent information on the zoögeography as well as paleontology and phylogeny of rattlesnakes. Mr. Klauber had planned to include revisions on a smaller scale throughout the work but his program was interrupted by illness early in 1968 and terminated by his death on May 8, 1968. Because of the continuing high demand for the volumes the Editorial Committee of the University of California Press has authorized the issuance of a revised edition of *Rattlesnakes* in the form in which Laurence Klauber left it. His thorough and meticulous methods of investigation and high standard of presentation more than justify such a decision. The Committee wishes to express its appreciation for counsel and guidance provided by Allan J. Sloan, Curator of Reptiles and Amphibians, San Diego Natural History Museum, in reviewing and preparing the second edition for the printer.

## Preface to the First Edition

In 1936, after having studied the classification of rattlesnakes for fifteen years, I published the results in the form of an identification key. I had previously noticed that these creatures commanded a sort of fearsome interest, even among people who certainly had no fondness for them. So I prefaced the key with a brief summary of rattlesnake ways of life, what they did and how, with the result that this pamphlet soon became an out-of-print rarity.

Obviously it was not the key to the identification of the different kinds of rattlesnakes that gave the booklet its brief popularity; rather it was the short discussion of the lives and habits of the snakes. And I had observed, although I myself never brought up the subject, that rattlers, despite—or maybe because of—their sinister reputations, would always bridge a dull spot in a dinner conversation. So in 1945 I began work on what was to have been a revision of the 1936 pamphlet, except that the identification keys were to be subsidiary to the observations on life history. As to the latter, I expected to dwell largely on a single species of rattlesnake—the western rattlesnake—which, in one of its several varieties, was the kind most often encountered by the covered-wagon emigrants westbound after crossing the Mississippi.

The present book has grown beyond the scope once contemplated. I hope that this expansion has not decreased its usefulness. Certain technical material of little interest to the casual seeker for the facts of rattlesnake life has been included; but throughout, the needs of this user have been kept in view. There has been a consistent effort—evidenced by a table of contents complete with every subject heading, a logical development of subjects by chapters, and an extensive index—to supply the needs of both the man who seeks some single fact to settle a bet, as well as the student with a broader purpose. In a way, this book is an encyclopedia of the rattlesnake; in it both the rattlesnake's reactions to its environment and man's reaction to rattlesnakes have been surveyed. Among other objectives, I have sought to disentangle rattlesnakes as they are from rattlesnakes as people imagine them to be.

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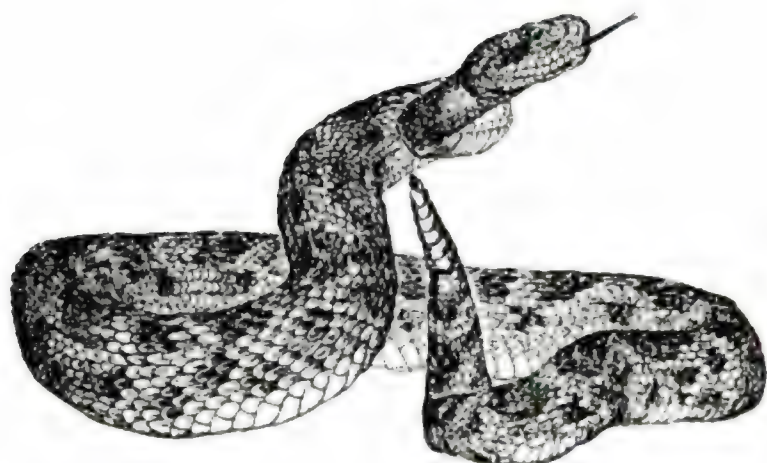
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## Introduction

Of all the books or pamphlets containing information about rattlesnakes, the two that have probably most influenced or guided public ideas on the subject were written by men who certainly never saw a rattlesnake in its native habitat, and may not even have seen one alive. These authors were Oliver Goldsmith and the Rev. John G. Wood, neither a naturalist, both rather inaccurate and credulous compilers, but each with the gift of interesting popularization. So cherished were their natural histories—first published in 1774 and 1851, respectively—that they appeared in unnumbered editions; they were reissued, reprinted, revised, enlarged, pirated, and quoted without credit. They were read avidly by the children of successive generations and remained the standard natural-history reference works in many British and American homes down to the present century. Their counterparts in German were the successive editions of Brehm's *Thierleben*; and, in French, some of the more popular abridgments of Buffon's *Histoire Naturelle*.

What made these and similar works so deservedly popular was not so much their vivid descriptions of the animals themselves as the information on their habits and the places where they live, often exemplified by stories of human encounters with them. It was not entirely the fault of these authors that many of their accounts were inaccurate, for naturally they were dependent for their information on the travelers abroad who had had the opportunity to make field observations. The compilers had no way of winnowing actual observations from the myths and tales the travelers brought back. This difficulty of separating fact from fiction is particularly formidable in the case of the rattlesnakes, creatures whose very nature invites exaggeration. Many of the rattlesnake stories still believed today date back to misunderstood incidents of colonial days, or to tales invented at the campfire to spoof a gullible traveler.

### PURPOSE AND SCOPE

This book is written to assemble and survey our present knowledge of rattlesnake habits and life histories. It is intended for reference rather than as a popular natural history of the rattlers, being, perhaps, too extensive and detailed for the latter purpose. But as it includes numbers of field observations from varied sources, it is hoped that it may aid in the correction of some of the dubious accounts long current in the popular natural histories; and, further, that it may encourage renewed

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investigations and observations respecting those phases of rattlesnake life now imperfectly understood or unknown. An effort has been made to keep the book from becoming overtechnical, with a view to making the individual sections into which it has been divided useful to any reader wishing further information on some particular aspect of rattlesnake life. The index should prove adequate to permit this sporadic type of reference.

I have no desire to exaggerate the importance of rattlesnakes in the scheme of nature, or in their influence on mankind. To people going afield—campers, hunters, fishermen, and the like—they constitute a relatively minor danger, yet the hazard is sufficient, or is believed to be, to cause many persons to suffer almost continuously from the fear of rattlers when in the woods or brush. An unexpected encounter with a rattler has broken up many a picnic party; the fear of meeting one has kept many another from ever leaving home. Those most familiar with these snakes learn to take them in their stride; they soon find that, compared with the hazard of a traffic accident, rattlesnakes constitute a negligible danger.

Along with their danger, real or imagined, rattlers are of economic value to the farmer or stock raiser by reason of their food habits, for they are predators on injurious rodents. They are handsome yet sinister creatures, with curious ways of life. They are expert performers on a musical instrument which they themselves cannot hear. I infer from the conversations of visitors at the Zoo, from letters of inquiry, and from the frequency of rattler items in the newspapers, that the general interest in them is great. In fact, throughout this book I have dwelt to a considerable extent on the relationships of rattlesnakes and men, for certainly one of the most remarkable aspects of rattlesnakes has been their effect on people. Quite apart, and often quite different, from their existence as reptiles in the forest or desert, rattlesnakes have had an existence in the minds of men—in unnatural natural history, in myth and folklore, in primitive medicine, and even in aboriginal religion. Certainly, the rattlesnake of song and story is a creature that quite surpasses nature. It is my hope that this book may lead to a better understanding of rattlesnakes, and this objective can only be achieved by a survey of some of the less accurate ideas, their sources, and their deviations from field experience.

Some may question the desirability of discussing herein so much that has been written about rattlesnakes that is untrue, varying from the mildly exaggerated to the fantastic. But if we are to know what to investigate and what to explain, we must know what beliefs people currently hold. And I find it rewarding to delve into the genesis of these beliefs. If it can be shown that some story originated with Pliny, then, by inference, it did not come from an observation on rattlesnakes, for none of the authors from whose works Pliny compiled his natural history had ever seen a rattler. This book is not only a survey of rattlesnakes, but of what people have thought about rattlesnakes and why; for these reactions and opinions are, in their way, as interesting as the snakes themselves are in another. And as these reactions are more often founded on ideas received through reading about or discussing snakes, than in observing them, it is important to know what has been said, and when, and by whom upon what knowledge. I hope that neither quotation nor reference will convey the idea that the beliefs are necessarily mine or are to be considered valid.

Men have attributed to rattlesnakes many powers that they do not have and exploits they could never have performed. These snakes are the subject of a large and curious body of folklore. They have long been a gold mine for the inventive storyteller at the chuck wagon. In some degree the folklore of the rattlesnakes—its persistence and the credulity of which it is an evidence—is more important than the ways of the snakes. Maybe credulity is the wrong word; it implies a sense of ridicule that is not intended. What I seek to convey is the fact of the persistence, the virtual indestructibility of natural history as created by gossip. Rattlesnakes are relatively unimportant creatures in our lives, and certainly no one can be criticized for not spending time in their study. Yet they must have an interest for people, for they will recount reputed experiences with rattlers on the slightest provocation. It is these stories that are a source of wonder and surprise, for seldom are they founded on more than hearsay; and that distorted by time and retelling. Such personal experiences as may be included are often themselves folklore, queerly transformed by repetition and the quirks of memory. How many times do we remember vividly, as personal experiences, family incidents that actually happened before we were born, so strongly does the early telling at the fireside imbed their pictures in our memories. As evidence of human methods of accumulating unverified beliefs, rattlesnake tales are not less interesting than the snakes themselves. It is as if we saw humanity reflected from a mirror of rattlesnakes, with all the peculiar effects caused by the undulations in the glass.

#### SOURCES OF INFORMATION

In the compilation of these life histories of the rattlesnakes, four sources of information have been available: (1) Correspondence with field observers and naturalists; (2) published accounts; (3) studies of captive rattlesnakes made at the San Diego Zoo; and (4) the personal observations of the writer in the field and laboratory.

*Data from Correspondents.*—There are certain people whose occupations keep them out-of-doors and in continuous contact with nature. They become naturalists in the best sense of the word. When they meet a rattler in the field it's a part of the day's work, not something to form the basis of a sensational story. Their observations are usually sound and accurate, in the aggregate comprising a volume of material far beyond the field notes of even the most fortunate and active herpetologist. What these observations may lack in co-ordination and continuity, they make up for in the corroborative evidence of their widespread sources.

About thirty years ago I conducted a campaign by mail to learn where certain kinds of rattlers were, or were not, found. This was for the purpose of mapping ranges with accuracy. More than a thousand letters and return postcards were sent to such persons as forest rangers, game wardens, and high-school biology teachers. Although the questionnaire was aimed primarily at settling problems of range boundaries, the form used contained a blank space for the entry of field notes. The replies proved so interesting that when the present book was first contemplated in 1945, I was encouraged to repeat the inquiry on a broader scale. This time over two thousand letters were sent out and more than five hundred replies were received. A variety of outdoor people were solicited for information, including

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National Forest rangers, U. S. Fish and Wildlife Service employees, Soil Conservation Service workers, National Park naturalists and rangers, and state game wardens and patrol officers. I am indebted to the headquarters staffs of many of these organizations for their courtesy in sending me the addresses of their field men. Other inquiries were sent to a miscellaneous list of field naturalists, hunters, trappers, stock and poultry raisers, county agricultural agents, and others likely to have firsthand information on the subject.

The form of inquiry, although suggesting various aspects of rattlesnake life upon which information was sought, avoided leading questions. After a trial series had shown the desirability of a change, a revised form made clear the fact that personal observations—actual field incidents—were sought, rather than generalizations upon rattlesnake life and habits. The results were most rewarding, and I cannot too gratefully acknowledge the valuable assistance received from these hundreds of correspondents. Many took the trouble to reply at length, giving in detail their experiences over many years. Some supplied the names of friends known to have information on the subject, and from these, in turn, information was requested. In many instances further correspondence was needed to clarify doubtful points, so that series of letters were involved.

Where possible, I have given the name, address, and the official connection of the person making any quoted statement. However, it should be remembered that some of the comments were received twenty or more years ago, and many addresses and positions have no doubt been changed in the interval.

The letters from which I have quoted are not restricted to the answers to these questionnaires. During the past years I have carried on an extended correspondence on the subject of rattlesnake life histories and habits with amateur and professional herpetologists who have had much experience with these snakes. From them I have secured many useful observations, which I have been privileged to quote.

There may be some criticism of what may seem unnecessary repetition in setting forth virtually similar experiences from several correspondents. This has been done with the deliberate intent of driving home the authenticity of certain observations, or the wide popular acceptance of others.

*Printed Material.*—My second source of information has been published material. I have examined a large number of books and articles, either about rattlesnakes or containing pertinent incidental statements on their habits. Some of these I have quoted verbatim; to many others I have made reference, summarizing the author's observations or conclusions, with an appropriate citation by page number so that any reader, consulting the bibliography, may locate the original statement.

Although some of the material abstracted from previous publications tends to confirm the observations of the correspondents I have quoted, others have reference to aspects of snake life that cannot be known from field observations alone, such as venom quality, snake growth and longevity, or sexual dimorphism. For these, the publications that I have quoted comprise the primary sources of data.

Admittedly the bibliography, although containing more than three thousand items, leaves much to be desired. It is definitely haphazard. The literature on

rattlesnakes is very extensive, for not only are there many technical articles on the subject, but there are the general natural histories, books of travel, medical journals, ethnological reports, nature magazines, the hunting and fishing periodicals, and, finally, the Sunday supplements, all containing material of interest, if not always of sound value. I have found only a part of these sources, and have included even fewer in the bibliography of this work.

Since this is primarily a discussion of rattlesnake life histories, I have omitted many treatises which, although important in their fields, have dealt mostly with rattlesnake squamation and classification—that is, they have their importance in the development of taxonomy and nomenclature. On the other hand, I have included many apparently ephemeral items, often of doubtful dependability, since they reflect popular beliefs concerning rattlers, and the facets of public interest. For these popular accounts of rattlesnakes in books, magazines, and newspapers are important, however much one may criticize their accuracy, since they indicate and accentuate the aspects of rattler life that are of the greatest interest to nonspecialists, and it is in part to satisfy these interests that the present work has been prepared. So I have included articles with whose conclusions I take issue, and whose sensational or exaggerated presentation I regret, but which do recount interesting occurrences or beliefs.

I have found that one cannot gauge the accuracy or importance of a contribution on rattlesnakes by the character of the publication in which it appeared. Some Sunday supplements have contained well-grounded articles, while, on the other hand, some of the worst offenders have been the journals whose presence on a reading table is presumed to add tone to the surroundings. Unfortunately, some of the nature writers whose works are duly acclaimed in the critical reviews deserve higher marks in English Literature 43 than in Biology 7. There are indications that a well-turned phrase sometimes distorts a field observation or conceals the lack of one.

I have found the sportsman's magazines particularly intriguing—especially the correspondence or question-and-answer columns. Some of the recurrent arguments—on how the rattler wears its rattles, for example—always bring out some useful observations in the heat of controversy. These arguments, by the way, seem never to be settled. After running through several successive numbers of a magazine they die down, only to be revived a year or so later by some new query in the same journal, as if the subject had never been discussed before.

There was hardly a traveler along the eastern seaboard in colonial days, or later any west-bound emigrant in a covered wagon, who did not make some comment on the rattlers seen or heard about. In the accounts of some of these travelers may be found the first expressions of some of the myths that persist to this day, but, on the other hand, many of their observations were quite accurate. I have quoted only a few of these; others may be located through Miss R. V. Medden's work (1929-31), from which I should acknowledge I received many good leads. I have also used many citations called to my attention by the late J. Frank Dobie.

This brings up the question of how so many relatively obscure articles were located. Bibliographies have a way of breeding like rabbits. Each new item, if it hasn't a bibliography of its own, is at least likely to contain a reference or two. Following these up has kept me flitting from library to library, of which I have

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worked in more than thirty—municipal, university, and specialized. Some items I never succeeded in running down. Many, whose titles were attractive, proved to be only recompilations of material previously exploited elsewhere.

A final reiteration on the bibliography: The references listed are not necessarily authoritative or accurate, and under no circumstances should the inclusion of an item be taken as indicating commendation or validity. Indeed, it may be a citation to serve as an example of inaccurate reporting. Nor is it claimed that the list is either well rounded or exhaustive. The venom and snake-bite phase alone, were completeness possible, would require a bibliography many times the size of the present one.

A word should be said about the manner of citing references. The method of inserting in the text—for example, Smith (1931, p. 61)—is, I think, more practical than the use of footnotes, for in reading, one soon learns to pass over such a citation unless it be desired to follow it up. Thus, footnotes have been reserved for incidental asides, and these have been kept to a minimum. Page references have been given whenever possible; how often have I boiled over when searching through a non-page-cited reference for a rattlesnake needle in a volume of hay. Also the publication, under one date, of an observation made many years before but not then printed, has been explained by dual date entries in most instances. However, these have not always been repeated. I trust that my references to Pliny, 1855–57, such being the dates of the translation I have used, will lead no one to misunderstand when this contemporary of Nero really lived, for he died in the eruption of Vesuvius that destroyed Pompeii, a victim of his desire for authentic field notes on an active volcano.

*Observations at the Zoo.*—Although the artificial conditions under which captive specimens live may distort their behavior patterns, it is still possible to gain many facts of value by observing them. Of this we have taken advantage at the San Diego Zoo, where thousands of rattlesnakes of many species have passed through our hands since 1922. The exhibit series at the Zoo comprises only a part of the many specimens kept under observation. Feeding and mating habits, venom yields, shedding, and other activities have been recorded, some of which can only be studied in captive specimens. C. B. Perkins and his successor, Charles E. Shaw, who have been in charge of the collection since 1932, have been unusually successful in simulating natural conditions, and their efforts have been rewarded with new records of longevity and of breeding in captivity. Under these circumstances many original or confirmatory data on rattler habits have been secured.

*Personal Field and Laboratory Experiences.*—Occasionally, in judging the dependability of articles on rattlers, I have wondered about the extent of the experiences of the authors and the backgrounds of their statements. Since many of my readers may mentally raise the same question respecting the validity of this compilation, I trust I may be pardoned for summarizing my own experience.

I have been interested in rattlesnakes for more than sixty years and during the past forty have put in whatever spare time has been available in a study of snakes in general and rattlers in particular. Some of this work has been in the field—for I have collected extensively in the Southwest—but more in the laboratory. Although these studies have been largely morphological or taxonomic, I have

recorded such field notes as have come my way. In connection with these studies, some of which have been published, I have accumulated scale counts, color notes, and measurements from about 12,000 rattlesnakes, of which some 7,500 were preserved in my own study collection, recently presented to the San Diego Society of Natural History. These large series have been useful in problems of subspecific differences and intrasubspecific variation. I have seen specimens of all of the kinds of rattlesnakes that are known to exist today, most of them alive. In the course of a venom-gathering program, I extracted the venom from somewhat more than five thousand live rattlers.

My training, however, has been in engineering, rather than in biology or medicine, and my lack of technical training in these fields has placed certain obvious limitations on this work. Particularly, the reader will find little on the physiology of the rattlesnakes, a subject that I should be ill-equipped to discuss. However, certain features such as fangs, lungs, squamation, rattles, male organs, and others of use in classification and phylogeny, are treated in some detail.

#### CO-ORDINATION OF DATA

In the process of arranging the observations and bibliographic references that comprise the bulk of this study, the most important preliminaries were, first a list of the subjects to be treated, and secondly the decision whether to group the data by subjects or by rattlesnake species. The first part of the program was met by the preparation of a schedule of subjects, together with numerical guides. Correspondents' field notes, bibliographic references, newspaper clippings, and the like, were then indexed so as to fall into their proper categories. Some, because of the diversity of subjects discussed, fell into many categories.

The second decision involved the treatment of species differences. The several species of rattlesnakes vary much more in their physical characteristics and habits than is commonly supposed, and it is quite impossible to generalize upon them without a sacrifice of accuracy. But most people are interested in rattlesnakes as a group rather than in their species differences. Therefore it was decided, in order to make the data more readily accessible, to discuss characteristics and habits as far as possible without reference to species differences, only segregating the material by species when made necessary by the extent of the variations between species, as in such subjects as size, food, habitats, snake-bite danger, and the like. And even in these cases I have first generalized with respect to the group as a whole, before listing the species peculiarities. In the subsequent discussions, species by species, some repetition has been inevitable, but it is only by this means that a reader, bent on seeking the life history of a single species, may locate the material desired.

#### EDITORIAL DISCRETION

Some editorial revision has, of course, been necessary in quoting my correspondents; their permission for this was requested in advance. Occasionally the observations were somewhat unco-ordinated or repetitive; these I have rearranged. It has not always been possible to break a statement down completely by subject without losing the sense of what the writer sought to convey, so some overlapping remains, some comments under one subject being really applicable to another. I regret this seeming lack of consistency.

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It is far from my intention to hold any correspondent up to ridicule. In the few instances where the inclusion of an observation of highly doubtful character appears desirable to illustrate some common misunderstanding, the name of the correspondent has been omitted. This has not been done in the case of printed material, however inaccurate, since the author has placed himself on record.

As far as my knowledge of the subject permits, exaggeration, sensationalism, and emotionalism have been avoided. Rattlesnakes are too interesting in themselves to need any embellishment in the telling.

Of course, I should be the last to claim that my choice of quotations from my correspondents, or from previously published articles, has been entirely objective, for such is not the fact. To have failed to use the privilege of editorial selection would have seemed to indicate my belief in many a now-discredited myth or in some interpretation contrary to the most elementary observation. So the selection and arrangement of material has been largely subjective—to that extent I may rightly be accused of stacking the cards—although I have tried to validate the position taken, through the corroborative evidence of many correspondents, of the published statements of herpetologists of the past and present, or of laboratory experiments.

Some parts of this book are necessarily technical. I hope that this will not reduce its usefulness or interest to the nonspecialist—the reader who has only a casual curiosity about rattlesnakes and their ways. He will probably find it convenient to skip certain sections and even entire chapters—chapter 2, for example. But other chapters, particularly those that deal with the relationships of rattlesnakes and men, such as those on rattlers and Indians (chap. 16), or myths and folklore (chap. 18), and on how to avoid being bitten (chap. 13), will be found relatively non-technical, and, I hope, will have a general appeal. Throughout this work the word *myth* has been used in the popular sense of any unsubstantiated or inaccurate belief, idea, or theory, without implying any religious connotation.

I have tried, as far as possible, to make the index appropriate to a book of reference. Unfortunately, it has generally been necessary to exclude, except in groups, the names of persons, places, and Indian tribes. Since each kind of rattlesnake is mentioned from twenty to many hundreds of times, it has been impossible to cite every mention of each species. But an attempt has been made to cite the more important habits and characteristics of each.

The last word will never be said on any of these problems of habits. Too many are imperfectly known; and even where the knowledge is final and complete, it never catches up with the myth. Who the explorer may have been who was first informed by some Indian that a rattler's age could be told by the number of its rattles, we have no idea. Soares de Sousa heard it at least as early as 1587. Its truth was exploded early in the 1700's by investigators who found that a snake gets a new rattle every time it changes its skin, and that it does this oftener than once a year, and that, anyway, most adult snakes have lost an indeterminate number of rattles through breakage. But the facts have not caught up with the myth, to judge from expressions overheard at the Zoo reptile house. Most people still think the rattles tell the age. And so it is with the other myths, the tall tales of the campfire, and misunderstood ethnozoölogy. I hope that this book may aid the reader somewhat in winnowing rattlesnake fact from fiction.

In writing this book, I have been beset with a constant struggle to avoid anthropomorphisms, teleologisms, Lamarckianisms, and all the other pitfalls that afflict anyone trying to describe the habits of life and the diversities in form of such a creature as the rattlesnake. Granted that no rattler has the calculating astuteness of the crafty serpent of folklore and tradition, it is equally true that, in its pursuits of food and self-preservation, it is not an automaton with every action instinctive and stereotyped. The diversity of its responses to the conditions encountered, some new to its experience, indicates a power of choice; and it is difficult to set forth the alternatives that may be chosen, as well as the making of the choice, without the use of verbs that suggest thought, such as "prefer," "decide," "adopt," "select," and similar anthropomorphic narcotics. Yet a strict avoidance of these pitfalls tends to picture a creature without flexibility of action, whose every response can be as readily predetermined by a human observer as the stimulus that he, the man, may impose to produce it. Such a circumscribed creature, it seems to me, is almost as different from a true rattlesnake as is the malevolent and calculating serpent depicted in the early natural histories. A rattlesnake may not have the power to visualize an objective when it pursues a course that will attain one, but at least it has the power to make an unexpected response to a stimulus, as anyone who fails to consider such a possibility may learn to his regret.

#### ACKNOWLEDGMENTS

It is impossible to list here the many hundreds of correspondents who have so graciously contributed valuable personal experiences and data on rattlesnakes. Many names have been mentioned in connection with the quotations they have supplied. Then there are the libraries and their helpful staffs, and the scientific institutions from which thousands of specimens have been borrowed for examination. Nor should I fail to mention the field collectors who have supplied so many specimens for my own collection, and the laboratory assistants who have aided in preserving and examining them.

But there are a few to whom I am most deeply indebted, who must be mentioned individually. First there are the late C. B. Perkins and his successor Charles E. Shaw of the Zoölogical Society of San Diego, Charles M. Bogert of the American Museum of Natural History, and the late Karl P. Schmidt of the Chicago Natural History Museum. They read the manuscript almost in its entirety, and from them I received unnumbered critical comments and suggestions of the greatest value. They have ferreted out many an error that I should otherwise have blushed for; yet none that remains—and there will be many—should be charged against them, for innumerable last-minute changes and additions have been necessary. My thanks are also due Raymond B. Cowles, Robert C. Stebbins, Harry Tschopik, James A. Oliver, and Leda Klauber, who were kind enough to review certain chapters. Most of the text figures were prepared by Norman Bilderback, and the photographs and maps by Leslie C. Kobler. The chapter-heading vignettes are the work of my niece Mrs. Paul Wormser. Items supplied by others have been appropriately identified.

Translations were made for me by Clinton G. Abbott, Mary V. Conway, Alice K. Miller, Ralph J. Phillips, Robert Menzies, Mayme Swanson, Marie Sorenson Cummings, Joan Shaw, with lesser stints by others.

I wish to thank Laurence M. Huey for editing the names of mammals and birds, Reeve M. Bailey for data on Iowa bounties, and Lillian Guralnick and I. M. Moriyama of the United States Public Health Service for snake-bite statistics.

Bayard H. Brattstrom has kindly kept me advised concerning his researches into ophidian osteology and paleontology, and even arranged the schedule of his publications so that I might use his findings in this book.

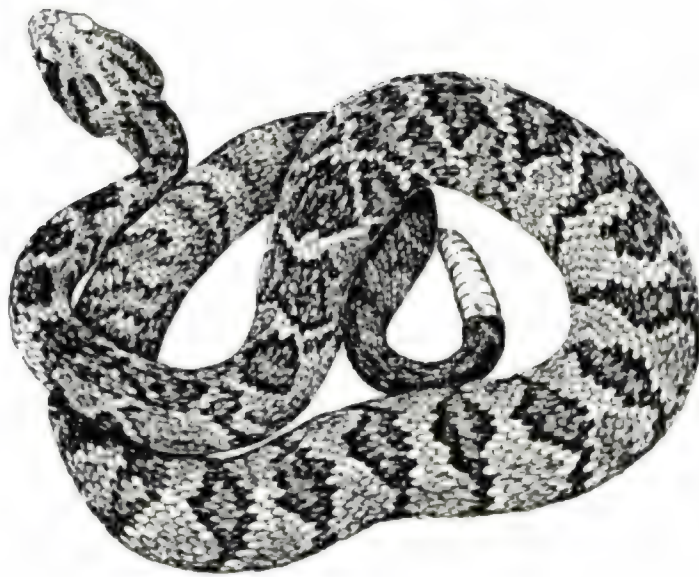
For field notes and observations, I am indebted to the innumerable correspondents whose names are scattered through the text, but I wish especially to mention A. C. Mackie, E. Ross Allen, and the late A. M. Jackley.

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## 1. Status

### INTRODUCTION

It is sometimes surprising to learn the extent to which the public may misunderstand basic terms. Thus, although the term "rattlesnake" is one familiar to every American, it is astonishing to find what different ideas people have as to the kinds of creatures that are included by the term. Some think all snakes are rattlesnakes, others that all venomous snakes are rattlers.<sup>1</sup> Some believe any snake that vibrates its tail when angry or alarmed to be a rattler, although in reality this is an attribute common to many kinds of snakes, both harmless and venomous. To obviate this confusion, and to permit the nonherpetologist to orient himself with respect to the position of the rattlesnakes in the snake world, this summary is presented.

### CLASSIFICATION AND NOMENCLATURE

Animals are classified by division into groups of successively narrowing scope. Thus the animal kingdom is divided into a few main groups, first into phyla, then the phyla into subphyla, and these, in turn, into classes. One of the classes of the subphylum Vertebrata, of the phylum Chordata, is the class Reptilia, which includes all the reptiles, living and extinct. Following down the line of increasingly restricted categories toward our objective, the rattlesnakes, we find the subclass Diapsida, then the order Squamata, and, finally, to separate the lizards from the snakes<sup>2</sup>—for both are included in the Squamata—the suborder<sup>3</sup> Serpentes, to which all snakes, venomous or harmless, belong. Suborders, in turn, are divided into families, and among others, under Serpentes, is the family Crotalidae or pit vipers, so called because of their possession of a remarkable sense organ visible externally as a facial pit, placed below and back of the nostril. By this family

<sup>1</sup> A similar idea is the application of the term "garter snake" to all harmless snakes in the United States, instead of specifically and properly to the snakes of the genus *Thamnophis*.

<sup>2</sup> Some lizards are without legs and look like snakes. They are differentiated from snakes by usually having eyelids and external ear openings, and no snake has either of these. Also, in all lizards, the two sides of the lower jaw are rigidly connected together in front, whereas in the snakes the connection is nonbony and flexible.

<sup>3</sup> K. P. Schmidt (1950, p. 79) prefers to raise the Squamata to the level of a superorder, Serpentes being correspondingly elevated to the status of a full order, as is also Sauria (the lizards). Bellairs (1957, p. 128) and Dowling (1959, p. 39) prefer to retain Sauria and Serpentes as suborders.

designation, the pit vipers are segregated from the true vipers of the family Viperidae,<sup>4</sup> which have no pits,<sup>5</sup> and which, incidentally, do not occur in the New World.

The next category below the family level is that of the genus (plural: genera). As our narrowing categories are now bringing us close to the two genera of rattlesnakes, their position with respect to their nearest relatives can best be clarified by recourse to table 1:1, which presents a summary of all of the genera belonging to the family Crotalidae.

Now we are in a position to define the term "rattlesnake" properly. Rattlesnakes are pit vipers—popular name for the whole family Crotalidae—belonging

TABLE 1:1  
THE COMPONENTS OF THE FAMILY CROTALIDAE

Genus	Common name	Distinguishing characteristics	Habitat
<i>Crotalus</i> .....	Rattlesnakes	With rattles; small scales on crown	North and South America
<i>Sistrurus</i> .....	Massasaugas and pigmy rattlesnakes	With rattles; large plates on crown	North America
<i>Lachesis</i> .....	Bushmaster	Without rattles; small scales on crown; small scales under end of tail	Central and South America
<i>Bothrops</i> <sup>a</sup> .....	New World pit vipers	Without rattles; small scales on crown; large scales under end of tail	Mexico to South America
<i>Trimeresurus</i> <sup>a</sup> ...	Asiatic pit vipers	Without rattles; small scales on crown	Asia
<i>Akistrodon</i> <sup>b</sup> ....	Moccasins	Without rattles; large plates on crown	North America, southeastern Europe, and Asia

<sup>a</sup> Some herpetologists include both the New and Old World snakes in the single genus *Trimeresurus*. Recent work on osteology by Ruiz (1951, p. 109), Brattstrom (1964a, p. 222), and others, indicates the propriety of the continued separation of *Bothrops* from *Trimeresurus*. Keys by which these genera may be differentiated will be found in chapter 2.

<sup>b</sup> This is sometimes spelled *Ancistrodon*. I believe *Akistrodon* to be proper, for reasons given elsewhere (Klauber, 1956, p. 258).

<sup>4</sup> Some herpetologists (e.g. Romer, 1956, p. 387; Bellairs, 1957, p. 148; Dowling, 1959, p. 50) split the pit vipers from the true vipers at the subfamily level, thus:

Family Viperidae—all vipers  
Subfamily Viperinae—true, or non-pit, vipers.  
Subfamily Crotalinae—pit vipers.

I prefer to consider the families Viperidae and Crotalidae as being separate, each with full family status. Such authorities as Johnson (1956, p. 58), Schmidt (1959, p. 83), Klemmer (1961, p. 362), and Brattstrom (1964a, p. 187) concur. The use of the word "true," in referring to the vipers without pits should not be taken to indicate that they are more properly termed vipers than those with pits. Both groups are vipers, the word "true" being used only to contrast with "pit."

<sup>5</sup> Several genera of the Viperidae—*Bitis*, *Pseudocerastes*, and *Eristocophis*—have a small hidden cavity, or sac, above the nostril that may have some genetic relationship with the pit of the pit vipers. It has been mentioned or discussed by Boulenger (1893-96, vol. 3, p. 493), Schmidt (1930, p. 228), Parker (1932, p. 222), Malcolm Smith (1943, p. 19), and Marx and Rabb (1965, pp. 169, 175, 181-184).

to the genera *Crotalus* and *Sistrurus*.<sup>6</sup> They are found only in the Western Hemisphere. All possess rattles. All are venomous, although, by reason of differences in size and other characteristics, there is a wide difference in the degree of danger from their bites. All are rather heavy-bodied and have broad heads. They are of various colors and are marked by blotches or by cross bands along the back. The plates under the tail are mostly in a single series, although a few plates may be split.

But above all, the crucial characteristic that distinguishes rattlesnakes from all other snakes—even from other pit vipers—is the possession of the rattle. This is a loosely articulated, but interlocking, series of horny rings at the end of the tail, which, when vibrated, produces a hissing sound. All rattlesnakes have rattles, and no other kind of snake has them. No snake is a rattlesnake because it is shaped like a rattler, or because it has blotches like those of a rattler, or because it is venomous, or because it is found among rattlers, or because it will coil like a rattler, or because it will vibrate its tail as does a rattler. Many harmless or venomous snakes have some or all of these characteristics, but lacking rattles, they are not rattlesnakes. The term “rattler,” as used in this book, is a short and popular synonym for rattlesnake; the term “rattle” refers only to the noise-making device at the end of the tail.

All rattlesnakes have rattles;<sup>7</sup> even when born they have a blunt segment called a prebutton, which, although soundless, is quite different from the pointed tail end of other young snakes. It is true that rarely—maybe once in a thousand—a rattler is found that has lost the end of its tail (including the rattle) in some accident. In most such instances, could the history be known, it would be found that someone, for a trophy, had cut the rattles off what he thought was a dead snake, after which it recovered. But in such cases there is no difficulty of identification because of the short stubby tail that remains, provided, of course, that it has the other characteristics of a rattlesnake.

There has been some confusion because of the coverage of the name of the family (Crotalidae), which includes the rattlesnakes; it has been mistakenly believed that all members of this family are rattlers. It is true that the family name was derived from the name (*Crotalus*) of one of the two genera of rattlesnakes, but this results from a rule governing the formation of family names. As will be seen from table 1:1, only two of the six groups of snakes belonging to the family Crotalidae are rattlesnakes; none of the others deserves the name, for none has rattles. It was probably this misunderstanding of the application of the family name, and reference to its members as crotalids, that led to the supposition that there are rattlesnakes in India (Corbyn, 1839, p. 929; Anon., 1883, p. 1209; Neog, 1951, p. 153), which is contrary to fact.

The two genera of rattlesnakes, *Crotalus* and *Sistrurus*, differ in the nature of the scales that cover the crown—the forward half of the top of the head. In *Sistrurus* this area is covered with large plates, usually 9 in number and regularly arranged in cross rows thus: 2—2—3—2, from front to rear (fig. 2:86). In *Crotalus* (fig. 2:87)

<sup>6</sup> Brattstrom (1964a, p. 239) considers *Crotalus* and *Sistrurus* to be subgenera of the single genus *Crotalus*, a classification which I do not favor.

<sup>7</sup> The Santa Catalina Island rattlesnake, restricted to a small, rocky island off the east coast of Baja California, usually has only a single rattle segment which covers the matrix at the end of the tail. There is no loose segment that can make a sound. This species will hereafter be termed the rattleless rattlesnake.

the crown is covered by small scales, particularly from the eyes rearward, although each eye generally has a single large plate (the supraocular) above it. Almost never, in *Crotalus*, is the space between the supraoculars occupied by a single large plate as in *Sistrurus*; instead, there are several or many small scales, usually quite irregularly disposed, occupying this region.

The genus *Crotalus* is the more important of the two; it includes the most species, the largest and most dangerous snakes, and ranges over much the greater territory. But the members of the genus *Sistrurus* are just as deserving of the name rattlesnakes, although, to distinguish them, they are generally referred to as massasaugas and pigmy rattlesnakes. Sometimes they are called ground rattlesnakes, not a particularly apt name as all rattlesnakes are ground dwellers.

The next lower category below the genus is the species, the fundamental unit of the divisional system. Each species is given a name composed of two parts, the first indicating the genus to which it belongs, the second the specific name applicable only to that species. (Examples: *Crotalus viridis* and *Sistrurus catenatus*.) Species, in turn, for the purpose of further segregation, may be divided into subspecies or races, in which case a third term, the subspecific name, is added. (Examples: *Crotalus viridis oreganus* and *Sistrurus catenatus tergeminus*.) Thus *Crotalus viridis oreganus*, the northern Pacific rattlesnake, is a subspecies of the more inclusive form, the western rattlesnake, *Crotalus viridis*, which in turn is one member of the genus *Crotalus*. The complete technical name of an animal also includes the name of the original describer and the date of the description, although these elements are often omitted in nontechnical articles, or where repetition makes the complete phrase unnecessary. (Example: *Crotalus viridis oreganus* Holbrook, 1840.) Often in longer works, where the same subspecies is repeatedly mentioned, only the initials of the first terms may be used and even these are omitted if there is no sacrifice of clarity. (Example: *C. v. oreganus*, or, simply, *oreganus*.) There is a rule requiring that technical names below the family level be italicized. Generic names are always capitalized; specific and subspecific names—in zoölogy, but not in botany—are never capitalized, even though derived from proper names.

The question arises as to how species and subspecies are segregated: Upon what bases are they differentiated? Species are populations that interbreed naturally; they cannot or will not interbreed with members of another species<sup>\*</sup> with which they may conjointly occupy a territory, and thus each preserves its separate identity and genetic integrity. It is found that these groups of rattlers—these species—differ from each other in one or more of a variety of ways: In adult size, in bodily proportions, in male organs, in pattern and color (the most obvious but not always the most valid difference), in osteology (especially of the skull), and, finally, in squamation—in the number of scales in certain series, and in their relative sizes, positions, and the contacts made with other scales. For rattlesnakes—in common with other snakes—are not clothed with scales haphazardly arranged like pebbles scattered on a beach. On the contrary, within each species the scales follow, with considerable consistency, certain patterns of size, number, and arrangement. These scale arrangements and counts are carefully studied to find species differences, especially to see if there is some particular difference that will serve as an invariable

<sup>\*</sup> Rarely there may be crossbreeding or hybridization, especially under the unnatural conditions of captivity.

guide—a key character, it is called—which will separate the individuals of one species from all others. The key character, be it understood, may be only one of a number of differences, but it is usually the one most readily detected. Key characters are seldom infallible, but they run true in a high percentage of cases. For example, in most specimens of the western rattlesnake, *Crotalus viridis*, there are three or more scales (internasals) at the forward end of the top of the snout between the nasal plates, whereas all other rattlers have but two. It should perhaps be noted that the structural characters may correspond to still more important physiological differences, some of which, like differences of blood serum and of venom, are readily discernible by experiment. But the scale differences are the most practical for purposes of classification, and most identification schedules or keys are largely based on them, as well as on color and pattern. Keys of this type will be found in chapter 2.

The differentiation between the subspecies of a single species is seldom as consistent and clear-cut as the differences between species. And even where the subspecies are well differentiated (if only specimens from their respective centers of population are considered) where these subspecific populations approach each other territorially, their differential characters will no longer be so clearly evident. Areas of intergradation are likely to be broad, with subspecies poorly differentiated, where ecological changes are also broad and gradual. Thus in these areas of intergradation the keys will not always be found effective in allocating a specimen to one or the other of the subspecies concerned.

#### A LIST OF RATTLESNAKE SPECIES AND SUBSPECIES

The list of rattlesnakes—that is, the number of species and subspecies—is continually growing, as new kinds are discovered in areas hitherto little explored, or as species are divided into more subspecies through the recognition of previously unnoted geographical divergences in characters. Nearly half of the subspecies now accepted have been described within the last 35 years. As of the present date, 31 existing species and 70 subspecies are recognized. Some are large, dangerous snakes while others are small with a less serious bite. Some are found in considerable numbers near populated areas or are distributed over wide territories. Others are restricted to a single island. Still others, although found on the mainland, occur in districts difficult of access to naturalists or collectors, so that only one or two specimens may ever have been seen by any herpetologist. There follows a list of the species or subspecies of rattlesnakes at present recognized as being valid:

#### RATTLESNAKES OF THE GENUS *CROTALUS*

- C. adamanteus* Beauvois, 1799. Eastern diamondback rattlesnake
- C. atrox* Baird and Girard, 1853. Western diamondback rattlesnake
- C. basilicus basilicus* (Cope),<sup>\*</sup> 1864. Mexican west-coast rattlesnake
- C. basilicus oaxacus* Gloyd, 1936. Oaxacan rattlesnake
- C. catalinensis* Cliff, 1954. Santa Catalina Island rattlesnake or rattleless rattlesnake

<sup>\*</sup>The insertion of parentheses around the name of the describer indicates that he originally assigned the species (or subspecies) to a genus other than the one in which it is now placed.

- C. cerastes cerastes* Hallowell, 1854. Mojave Desert sidewinder  
*C. cerastes cercobombus* Savage and Cliff, 1953. Sonoran Desert sidewinder  
*C. cerastes laterorepens* Klauber, 1944. Colorado Desert sidewinder  
*C. durissus durissus* Linné, 1758. Central American rattlesnake  
*C. durissus culminatus* Klauber, 1952. Northwestern Neotropical rattlesnake  
*C. durissus terrificus*<sup>10</sup> (Laurenti), 1768. South American rattlesnake  
*C. durissus totonacus* Gloyd and Kauffeld, 1940. Totonacan rattlesnake  
*C. durissus tzabcan* Klauber, 1952. Yucatan Neotropical rattlesnake  
*C. enyo enyo* (Cope), 1861. Lower California rattlesnake  
*C. enyo cerralvensis* Cliff, 1954. Cerralvo Island rattlesnake  
*C. enyo furvus* Lowe and Norris, 1954. Rosario rattlesnake  
*C. exsul* Garman, 1883. Cedros Island diamond rattlesnake  
*C. horridus horridus* Linné, 1758. Timber rattlesnake  
*C. horridus atricaudatus* Latreille, 1802. Canebrake rattlesnake  
*C. intermedius intermedius* Troschel, 1865. Totalcan small-headed rattlesnake  
*C. intermedius gloydi* Taylor, 1941. Oaxacan small-headed rattlesnake  
*C. intermedius omiltemanus* Günther, 1895. Omilteman small-headed rattlesnake  
*C. lannomi* Tanner, 1966. Autlán rattlesnake  
*C. lepidus lepidus* (Kennicott), 1861. Mottled rock rattlesnake  
*C. lepidus klauberi* Gloyd, 1936. Banded rock rattlesnake  
*C. lepidus morulus* Klauber, 1952. Tamaulipan rock rattlesnake  
*C. mitchellii mitchellii* (Cope), 1861. San Lucan speckled rattlesnake  
*C. mitchellii angelensis* Klauber, 1963. Angel de la Guarda Island speckled rattlesnake  
*C. mitchellii muertensis* Klauber, 1949. El Muerto Island speckled rattlesnake  
*C. mitchellii pyrrhus* (Cope), 1866. Southwestern speckled rattlesnake  
*C. mitchellii stephensi* Klauber, 1930. Panamint rattlesnake  
*C. molossus molossus* Baird and Girard, 1853. Northern black-tailed rattlesnake  
*C. molossus estebanensis* Klauber, 1949. San Esteban Island rattlesnake  
*C. molossus nigrescens* Gloyd, 1936. Mexican black-tailed rattlesnake  
*C. polystictus* (Cope), 1865. Mexican lance-headed rattlesnake  
*C. pricei pricei* Van Denburgh, 1895. Western twin-spotted rattlesnake  
*C. pricei miquihuanus* Gloyd, 1940. Eastern twin-spotted rattlesnake  
*C. pusillus* Klauber, 1952. Tancitaran dusky rattlesnake  
*C. ruber ruber* Cope, 1892. Red diamond rattlesnake  
*C. ruber lucasensis* Van Denburgh, 1920. San Lucan diamond rattlesnake  
*C. scutulatus scutulatus* (Kennicott), 1861. Mojave rattlesnake  
*C. scutulatus salvini* Günther, 1895. Huamantlan rattlesnake  
*C. stejnegeri* Dunn, 1919. Long-tailed rattlesnake  
*C. tigris* Kennicott, 1859. Tiger rattlesnake  
*C. tortugensis* Van Denburgh and Slevin, 1921. Tortuga Island diamond rattlesnake  
*C. transversus* Taylor, 1944. Cross-banded mountain rattlesnake  
*C. triseriatus triseriatus* (Wagler), 1830. Central-plateau dusky rattlesnake  
*C. triseriatus aquilus* Klauber, 1952. Queretaran dusky rattlesnake  
*C. unicolor* Van Lidth de Juede, 1887. Aruba Island rattlesnake  
*C. vegrandis* Klauber, 1941. Uracoan rattlesnake

<sup>10</sup> See footnote 7, page 13.

- C. viridis viridis* (Rafinesque), 1818. Prairie rattlesnake  
*C. viridis abyssus* Klauber, 1930. Grand Canyon rattlesnake  
*C. viridis caliginis* Klauber, 1949. Coronado Island rattlesnake  
*C. viridis cerberus* (Coues), 1875. Arizona black rattlesnake  
*C. viridis concolor* Woodbury, 1929. Midget faded rattlesnake  
*C. viridis helleri* Meek, 1905. Southern Pacific rattlesnake  
*C. viridis lutosus* Klauber, 1930. Great Basin rattlesnake  
*C. viridis nuntius* Klauber, 1935. Hopi rattlesnake  
*C. viridis oreganus* Holbrook, 1840. Northern Pacific rattlesnake  
*C. willardi willardi* Meek, 1905. Arizona ridge-nosed rattlesnake  
*C. willardi amabilis* Anderson, 1962. Del Nido ridge-nosed rattlesnake  
*C. willardi meridionalis* Klauber, 1949. Southern ridge-nosed rattlesnake  
*C. willardi silus* Klauber, 1949. West Chihuahua ridge-nosed rattlesnake

### RATTLESNAKES OF THE GENUS *SISTRURUS*

- S. catenatus catenatus* (Rafinesque), 1818. Eastern massasauga  
*S. catenatus edwardsii* (Baird and Girard), 1853. Desert massasauga  
*S. catenatus tergeminus* (Say), 1823. Western massasauga  
*S. miliarius miliarius* (Linné), 1776. Carolina pigmy rattlesnake  
*S. miliarius barbouri* Gloyd, 1935. Dusky pigmy rattlesnake  
*S. miliarius streckeri* Gloyd, 1935. Western pigmy rattlesnake  
*S. ravus* (Cope), 1865. Mexican pigmy rattlesnake

It will be observed that there are only two popular names that do not involve the use of the term "rattlesnake"; these are "sidewinder" and "massasauga." The name sidewinder is derived from the snake's peculiar method of crawling. The term massasauga is said to have been derived from the Mississauga Indians and Mississauga (also spelled Mississagi) River, in Ontario, Canada. Applied to this species of rattlesnake, and spelled massasaugua, it was used as early as 1838 by Kirtland (p. 190), who said it was a popular name for this rattler at that time. Ingersoll (1883a, p. 35) and Atkinson and Netting (1927, p. 40) state that the name was derived from two Chippewa Indian words meaning "great river mouth." Presumably, this would have reference to the swampy habitat of both the Mississauga Indians and this species of rattlesnake.

### VENOMOUS SNAKES IN THE UNITED STATES OTHER THAN RATTLESNAKES

Thus far I have pointed out the category in which the rattlesnakes fall as members of the family Crotalidae, and have listed the nonrattler genera in that family, as well as the rattlesnakes themselves. Another approach is justified—a glance at the position of the rattlesnakes in relation to the other venomous snakes found in the United States. For rattlesnakes are not the only poisonous snakes in the United States, although it is true that, as a group, they are the most widespread, the most prevalent in numbers, and, because of the size attained by some species, the most dangerous.

The distinction between the world's venomous and harmless snakes is neither as sharp nor as easy to ascertain as is often presumed. There is no ready means of telling, from a superficial examination, whether a snake is venomous. Not all poisonous snakes are heavy-bodied with broad, triangular heads, as is commonly supposed. On the contrary, some very dangerous snakes abroad—the mamba of Africa, the Indian cobra, the Australian tiger snake, for examples—are not greatly different in form from our harmless racers and bull snakes. But, fortunately, in the United States there is a ready means of identification applying to all of our dangerously venomous snakes except one group—the coral snakes. The rest, including the rattlers, are all pit vipers, and have the characteristic facial opening below and behind the nostril which gives them that name. In this country, as is the case everywhere except in Australia, the harmless snakes greatly outnumber the venomous, both in number of kinds and in number of individuals.

I have already commented on the lack of a sharp distinction between harmless and poisonous snakes. There are, in this country, as in many others, snakes that are, technically speaking, venomous, but which are quite harmless to man. They have venom glands and fangs, but the fangs are located in the back instead of in the front of the upper jaw. The fangs are short and are grooved, rather than hollow. In consequence, they can only be imbedded in things of relatively small diameter, such as lizards and the other small creatures upon which these snakes feed, and they must chew the victim, rather than merely biting it, to get the venom into the wound. The largest of these back-fanged species found in the United States and their ranges here are as follows:

*Trimorphodon lambda* Cope, 1886. Sonoran lyre snake. Southwestern Utah, southern Nevada, and southeastern California, southeast through central and southern Arizona, to southwestern New Mexico.

*Trimorphodon vandenburghi* Klauber, 1924. California lyre snake. Coastal and desert southern California.

*Trimorphodon vilkinsoni* Cope, 1886. Texas lyre snake. Extreme western Texas and south-central New Mexico.

*Leptodeira septentrionalis septentrionalis* (Kennicott), 1859. Texas cat-eyed snake. Extreme southern Texas.

*Coniophanes imperialis imperialis* (Kennicott), 1859. Black-banded snake. Extreme southern Texas.

*Oxybelis aeneus auratus* (Bell), 1825. Mexican vine snake. Extreme southern Arizona.

There are other, still smaller, back-fanged snakes in the United States that I have omitted; their bites could not be serious to man.

As I have said, I doubt whether the bite of any of these back-fanged species, because of their inefficient venom-injecting mechanisms, could be serious to a man unless he deliberately put a finger in the snake's mouth and allowed the snake to chew it. I hope that my inclusion of these relatively rare snakes in this list of venomous snakes will not lead to the killing of a lot of quite harmless and useful creatures. In some Old-World countries there are back-fanged snakes whose bites can be fatal.

In passing on to the really dangerous snakes of the United States, it may be observed that the most striking thing about venomous snakes, and, in a way, the most important, is not the venom itself but the efficient means for injecting it. True, the venom in some species is exceedingly powerful, and if injected into the blood stream of a victim produces disastrous results. But this is true of many protein substances, the white of an egg, for example, or the blood of an unrelated animal. Alcock and Rogers (1902, p. 446; see also Noguchi, 1909, p. 51; Winton, 1916, p. 477; Marie Phisalix and Caius, 1916, p. 213; 1917, p. 37; Bragg, 1960, p. 121) found the parotid secretions of certain harmless snakes to be decidedly toxic. But they are harmless because they lack the means for its injection. And so among the venomous snakes, particularly the true vipers and pit vipers, the most amazing development is not so much the venom as the highly specialized means for its injection into the prey—that is, the venom glands, ducts, and fangs, which, together, comprise natural hypodermic syringes of great efficiency.

One frequently hears the statement that there are four “kinds” of dangerously venomous snakes in the United States—coral snakes, copperheads, water moccasins, and rattlers. This, however, is a rather inaccurate way of putting it, for if we group the coral snakes together, or the rattlers, we ought likewise to group the moccasins—the copperhead and water moccasin—since these two are more nearly related to each other than are some of the coral snakes to each other, or some of the rattlers among themselves.

The number of kinds of dangerously venomous snakes that there are in the United States depends on the interpretation of “kinds.” On the family level there are two—the Elapidae and Crotalidae (coral snakes and pit vipers). On the generic level there are five—*Micrurus*, *Micruroides*, *Agkistrodon*, *Sistrurus*, and *Crotalus*. If we pass on to the species level there are no less than 19, and of subspecies there are 42 venomous kinds in the United States, counting only the front-fanged forms. At no level are there four, except in the application of common names.

To complete this account of the front-fanged venomous snakes in our country, I list those that are not rattlers:

*Micrurus fulvius fulvius* (Linné), 1776. Eastern coral snake. From southern Florida north to North Carolina, and west to the Mississippi River.

*Micrurus fulvius barbouri* Schmidt, 1928. South Florida coral snake. Extreme southern Florida. (The validity of this subspecies is questioned by Duellman and Schwartz, 1958, p. 315).

*Micrurus fulvius tenere* (Baird and Girard), 1853. Texas coral snake. Arkansas to southern Texas.

*Micruroides euryxanthus euryxanthus* (Kennicott), 1860. Arizona coral snake. Southern Arizona, southwestern New Mexico, extreme western Texas, and southwestern Utah; the last is to be considered a doubtful locality.

*Agkistrodon contortrix contortrix* (Linné), 1766. Southern copperhead. Eastern Texas to North Carolina.

*Agkistrodon contortrix mokasen* (Beauvois), 1799. Northern copperhead. Eastern Kansas and Nebraska to Massachusetts.

*Agkistrodon contortrix laticinctus* Gloyd and Conant, 1934. Broad-banded copperhead. Central Texas to southern Kansas.

*Agkistrodon contortrix pictigaster* Gloyd and Conant, 1943. Trans-Pecos copperhead. Trans-Pecos Texas.

*Agkistrodon piscivorus piscivorus* (Lacépède), 1789. Eastern cottonmouth moccasin. Southeastern Virginia to southern Florida and west to eastern Mississippi.

*Agkistrodon piscivorus leucostoma* (Troost), 1836. Western cottonmouth moccasin. Southern Texas and Mississippi Valley, north to southern Illinois.

The coral snakes, which are allied to the cobras of the Old World, have a powerful venom. However, they are usually mild-tempered creatures, and their fangs are relatively short; such accidents as have occurred have nearly always resulted from carelessly and even roughly handling them. Allen and Merryday (1940, p. 239) mention a man who carried a coral snake in one hand, not knowing it was dangerous, while driving a car several miles with the other. These are pretty snakes and their harmless appearance constitutes their greatest danger. They are not so important a hazard in the United States as is often supposed because of their relationship with the cobras of the Old World. Out of 104 fatalities from snakebite in the United States during the ten-year period 1950-1959, only two were caused by coral snakes (Parrish, 1963a, p. 36). See also Neill (1957, p. 111) and McCullough and Gennaro (1963b, p. 938). The Arizona coral snake is smaller than the species occurring from Florida to Texas. The few human cases of the bite of *M. e. euryxanthus* that are known indicate that a bite may possibly be serious, despite the diminutive size of the snake.

The cottonmouths and copperheads have much the same shape as rattlesnakes, except that they are without rattles and have tapering tails. The bite of a cottonmouth is about as dangerous as that of a rattlesnake of similar size. The bite of a copperhead is painful and requires treatment, but human fatalities caused by this snake are extremely rare. In the ten-year period 1950-1959, none of the 104 fatalities from snakebite in the United States resulted from a copperhead bite, although many people had been bitten by them (Parrish, 1963a, p. 36).

Rumors of other kinds of dangerously venomous snakes in various parts of the United States are occasionally heard, such as an escaped colony of Australian tiger snakes or Indian cobras on the Pacific Coast, or a mysterious viper called the "pichicuate" in the southwestern states. There is no foundation for any of these stories, most of which are based on a misidentification of harmless snakes.

#### CONFUSION REGARDING RATTLESNAKES

I mentioned initially a rather widespread confusion that exists with regard to rattlesnakes. I did not have in mind any uncertainty respecting the taxonomic position of the rattlers among the venomous snakes or a confusion between species of rattlers. These, after all, are problems for the specialist. What I had in mind was the inability of many persons to distinguish rattlers from quite harmless snakes, or from other kinds of venomous snakes; in other words, an uncertainty as to just what is a rattlesnake.

This confusion between supposed rattlesnakes and the real thing may have various important consequences. It leads to the killing of harmless snakes having considerable economic value, and whose destruction may actually increase the rattle-

snake population because there will then be fewer harmless snakes competing with the rattlers for food. It leads to serious complications in snake-bite cases, for the proper treatment of rattlesnake bite is, in itself, a painful procedure, and, if unnecessarily undertaken, puts the patient to great discomfort and some hazard. Further, the psychological effects of the bite of a harmless snake mistaken for a rattler may be quite serious. Such cases are well authenticated in the medical literature. In one instance in San Diego County, a man bitten by a harmless gopher snake—which he thought was a rattler—almost died of shock. Kahn (1942, p. 288) believes that a considerable proportion of fatalities from snake bite in India are caused by shock rather than venom, owing to difficulties of identification and a quite erroneous belief there that all snakes are venomous.

Finally, these mistakes of identification are the bane of the snake specialist. He gets reports of the presence of rattlers in areas where they presumably never existed, or have long since been exterminated, and when he runs these down the only evidence usually found is the smashed body of some harmless snake. Bogert (1948b, p. 187) reported that, during the previous 10 years, of nearly 100 snakes that were brought into the American Museum of Natural History on the supposition that they were venomous, actually only 3 proved to be, including one rattler and 2 copperheads. At San Diego, where no venomous snakes other than rattlesnakes occur, it is surprising how many specimens are brought to the zoo as rattlesnakes, that prove to be harmless species. Kenneth C. Johnson, a police official at Sacramento, who investigated complaints by citizens that there were rattlers on their premises, found, out of 10 reports, that only 2 were really rattlesnakes; the remaining 8 were harmless gopher snakes. Some of the inaccurate field notes on rattlesnakes are based on observations of quite different snakes that were mistaken for rattlers. No doubt a few of my correspondents may have been misled in this way, but I think most of them, by reason of their outdoor vocations, were beyond making such mistakes.

Much of the confusion as to just what a rattlesnake is, arises from two sources—a misunderstanding concerning the dispositions and actions of harmless snakes, or a misapplication of names.

Many persons think that all venomous snakes are aggressive, or even vicious and vindictive creatures, whereas harmless snakes are thought to be kindly and timid. So, when they see a harmless garter or bull snake go through all the actions usually attributed to a rattler, such as coiling and striking, flattening the body and hissing, and even vibrating its tail—which, if done among dry leaves, makes a fair imitation of a rattle—they jump to the conclusion that the snake is a rattler, or at least a close relative, even though it lacks the telltale appendage on the tail. This is the source of the widespread myth, particularly prevalent in the intermountain states, to the effect that the rattlers have interbred with bull snakes, producing a peculiarly vicious and dangerously venomous offspring. The fact that the bull snake is blotched adds to the fancied resemblance to the venomous one of the mythical parents. But there is not the slightest indication that such a hybrid has ever been produced or is possible."

"It is unfortunate that a supposedly authoritative work should increase this confusion by the misuse of a common term for a certain kind of venomous snake, as is done when it refers to the harmless bull or gopher snake as "a handsome viper." I refer to *American Guide Series: Idaho* (1937, p. 130).

As a matter of fact, many harmless snakes, when cornered, will put on just as spectacular a posture of defense as any rattler—more so, in fact, since the threat is purely a bluff, not backed, as is the rattler's, by any really potent weapon. The red racer, for example, is generally quite aggressive, biting fiercely on the slightest provocation. But the bite is harmless—no more serious than a series of pin pricks. A cornered gopher or bull snake is the picture of a vindictive and dangerous creature. It coils and vibrates its tail, and lunges repeatedly at any intruder. It hisses violently, having a peculiar construction of the epiglottis that accentuates the sound. This frightening pose will quite convince an observer that so ferocious an animal had best be let alone, which is exactly its purpose. But it is all bluff; and the difference between being struck by a gopher snake and a rattler is the difference between being hit by two falling objects—a feather in one case, a safe in the other.

Part of the confusion arises from a misunderstanding to the effect that the rattle is not always present. Some of the early naturalists advanced the theory that rattlesnakes do not get their first rattles until they attain their third year (Clayton, 1693, p. 126). Others had been told by Indians that only the males have rattles (J. F. D. Smyth, 1784, p. 108); and still others thought that rattlers were without their rattles during part of each year. Whoever might believe this would have no trouble in convincing himself that some threatening but harmless snake on the defensive was a rattlesnake without rattles.

Another cause of confusion is the failure of the supposed criteria for segregating venomous snakes—particularly rattlers—from the harmless: the broad head, thick body, and vertical pupil. Since these characteristics are also possessed by many harmless snakes, confusion is inevitable.

A further source of misunderstanding of what a rattlesnake really is, lies in the misapplication or misunderstanding of popular terms. For example, in some areas certain harmless snakes are known as rattlesnake pilots (see under myths, p. 1275) and this is often followed by confusion with the rattlesnakes themselves. In other sections of the country, not only are all small rattlesnakes called sidewinders—although they are not the true sidewinder, or horned rattlesnake, of our southwestern deserts—but even some harmless snakes become known as sidewinders, and therefore are confused with rattlesnakes. In still other areas, all snakes that vibrate their tails when alarmed—a common habit of many harmless snakes, as well as venomous snakes other than rattlers—are popularly known as “ground rattlesnakes” (Strecker, 1935, p. 27).

Much more readily understood and excused are the confusions between various species and subspecies of rattlesnakes. Since professional herpetologists sometimes experience difficulty in distinguishing between them, or in agreeing upon their proper classification, there need be no wonder that foresters, hunters, and fishermen should have the same trouble. So it is, that in places where two or more species of rattlers are found together—and there are some places where as many as 5 or 6 occur—there is often confusion between them, accentuated by the inexact use of common names. It is equally true that in some areas where there is only a single kind of rattler, many persons believe there are two, because of fancied or actual variations in average size, temperament, color, or pattern. For example, John Muir thought there were two species in Tuolumne Canyon, California, evidently be-

cause of the difference between the brightly colored juveniles and the duller adults (Wolfe, 1938, p. 344). As a matter of fact, only the northern Pacific rattlesnake (*C. v. oreganus*) occurs there.

#### DISTINGUISHING VENOMOUS FROM HARMLESS SNAKES

The difficulties of distinguishing venomous from harmless snakes are by no means confined to rattlesnakes; quite the contrary, for the rattlesnake, through possession of the rattle, is the most easily recognized of all venomous snakes. It is unfortunate that there is not some simple criterion by which the poisonous character of any venomous snake might be made readily apparent, but there is none. As a matter of fact, there is no sharp line dividing the venomous and harmless forms, for, as I have mentioned before, snakes pass by degrees from the purely harmless through the back-fanged species, some of the largest of which are definitely dangerous, to the front-fanged and the folding-fanged snakes, to which groups nearly all of the really dangerous species belong. But even of these there are some that, because of small size, short fangs, mild venom, or like reasons, produce hardly as serious a result as a bee sting. One point should be understood—that none of the popular criteria such as a broad, triangular head, a heavy body, cat's eyes (vertical pupils), a flat body, or rough scales, are safe criteria, since there are both harmless and dangerous snakes known with any or all of these characteristics. Occasionally, in some restricted district, the particular snake fauna found there may permit the use of some such simple rule, but this is rarely the case. The only unfailing method is an examination of the snake for hollow or grooved fangs and venom glands, and even this will not disclose the degree of the danger from its bite.

As early as 1796, P. Russell (p. vi) pointed out that it was difficult to get accurate information about Indian snakes because of a confusion of names and descriptions. Nicholson (1874, p. 158) said that, in India, neither the natives nor Englishmen could distinguish venomous from harmless snakes. This is a common difficulty in most countries where there are many different kinds of snakes. It is not unusual to find that harmless snakes, through some imaginary attribute, are more feared than those that are truly dangerous; and resemblances to venomous snakes, either fancied or real, are the source of much confusion. Because of the colors of their rings, in California the long-nosed snake (*Rhinocheilus*), the mountain kingsnake (*Lampropeltis zonata*), and the shovel-nosed snake (*Chionactis*), are all feared as coral snakes, although no true coral snake occurs in that state.

#### THE USE OF COMMON NAMES

I shall, in discussing the rattlesnakes in the succeeding chapters, use common names to indicate the several species, usually following this with the technical name as well. I do this in recognition of the fact that most people dislike technical names, partly because of unfamiliarity with them, but also because their use is deemed an academic affectation upon the part of scientists. The latter is far from being the case. On the contrary, technical names are preferred because their composite nature indicates certain relationships, and because they are more stable and precise. For there is a code of rules and an international authority governing their promulgation and use. True, an occasional name, because of the conditions surrounding its original application, may be the subject of some uncertainty and dis-

pute; but, by and large, the great body of naturalists in any field agree upon almost all the technical names applied to the animals they study.

With respect to popular names, on the other hand, there is no order, agreement, or stability. At least as far as herpetology is concerned, no recognized authority has yet stepped in to recommend a co-ordinated set of names for adoption.<sup>12</sup> Thus each author is free to adopt any that he chooses; and although he may conscientiously try to follow the suggestions of his predecessors and colleagues, he is beset with duplications, uncertainties, and confusions, complicated by local usages. For example, the snake that I call the northern Pacific rattlesnake (*Crotalus viridis oreganus*) is variously known, in different parts of California, as the black, black diamond, diamondback, green, gray, mountain, rock, and timber rattlesnakes, to mention only a few of its names. And, worse yet, a quite different snake occurring in Florida is better entitled to the name "diamondback" than is *oreganus*, and still another in the eastern United States is generally and properly called the timber rattlesnake. Other examples may readily be cited. Atkinson and Netting (1927, p. 40) list the following names as being applied to *Sistrurus catenatus catenatus*: massasauga, black snapper, swamp rattler, pigmy rattler, black massasauga, black rattler, prairie rattler. The last name, although quite generally applied to this snake in the central part of its range (Lyon and Bishop, 1936, p. 253), is a particularly bad choice since it is the usually accepted name of a quite different snake, *Crotalus viridis viridis*, which ranges throughout the Missouri River basin. A similar confusion is contained in Branson's *Snakes of Kansas* (1904, p. 355). Geare (1903, p. 137) says that *S. c. catenatus* is sometimes called the sideler or sidewiper because of its habit of wriggling sideways. Even as definite and well-earned a name as that of the true sidewinder (*Crotalus cerastes*)—so called because of its peculiar method of crawling—is now generally misapplied to the young of almost any western rattler. In fact, a recent poll at the San Diego Zoo showed that the name is considered by many to be a nickname for any rattlesnake.

These multiplications and confusions of names are by no means new. In 1653, Jonstonus (p. 26) listed the following alternative names for the South American rattlesnake: boicininga, boiquira, cascavella, tangedor, teutlacocauhqui, and domina serpentum.

This conflict of names I shall try to surmount by adopting for the purposes of this book the set of popular names already presented in this chapter. These I shall employ consistently in deference to those who prefer them to the Latin names. But often I shall use both names with the idea of achieving definiteness and also to increase the reader's familiarity with the technical names. In some cases—tabulations, for example—technical names are essential for condensation; compare for instance "*C. m. pyrrhus*" with "southwestern speckled rattlesnake," or "*ruber*" with "red diamond rattlesnake." In some of the more technical sections of this book, I have, for the sake of clarity and brevity, used technical names almost exclusively.

This matter of rattlesnake names, and the use of methods whereby the same creature will be identified by the same name by everyone, is by no means solely of

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<sup>12</sup> Such a standardized list of names has now been supplied for the amphibians and reptiles found in the United States. (See Conant, Committee Chairman, 1956, p. 172).

academic interest. Where several species of rattlesnakes occur together in a locality, it might be of great value to a physician treating a case to know which one had caused the bite. In the future, snake-bite treatment will increasingly recognize the great differences in venom quality among the several species of rattlesnakes, as well as other species differences affecting the gravity of the bite.

Many other kinds of snakes are confused by a similar lack of standardization of names. For example, both harmless and venomous snakes are known as water moccasins (Yarrow, 1883, p. 263; Coleman and Gratacap, 1897, p. 311). Wright (1950, p. 141) has listed the common names applied to the snakes of the United States, and has shown the extent of the confusion and overlapping that exists in the use of such names.

Some of the matters of identification and names that I have discussed are commented upon by several of my correspondents:

There are many lakes and streams near here, and near them are water and bull snakes. A great many people see some of these harmless snakes and mistake them for rattlesnakes. *Jack I. Groom, U. S. Forest Service, Lakeview, Oreg.*

Even common harmless snakes, as the fox snake, are frequently mistaken for rattlers, and called in some parts of Ontario, the hardwood rattler. The hog-nosed snake is often killed throughout the northeast, and is called a copperhead. Some people recently killed a snake out in the center of Long Island, where rattlesnakes were to be found a generation ago, and thought it was a rattlesnake, but it proved to be only a harmless milk snake. *H. E. Miller, Stratford, Conn.*

The enormous numbers of *Natrix sipedon* (a harmless water snake) which we saw on Stony Island may have something to do with the tales told of massasaugas supposed to be there. The natives will not go near the island for fear of snakes. But we got only five rattlers in a full day's earnest search. *Gordon L. Walls, Ann Arbor, Mich.*

Of course, these confusions of names and identifications represent only a small part of the misunderstandings and exaggerations that have obscured our knowledge of the rattlesnakes from the earliest days. Some have resulted from such fantastic statements as these:

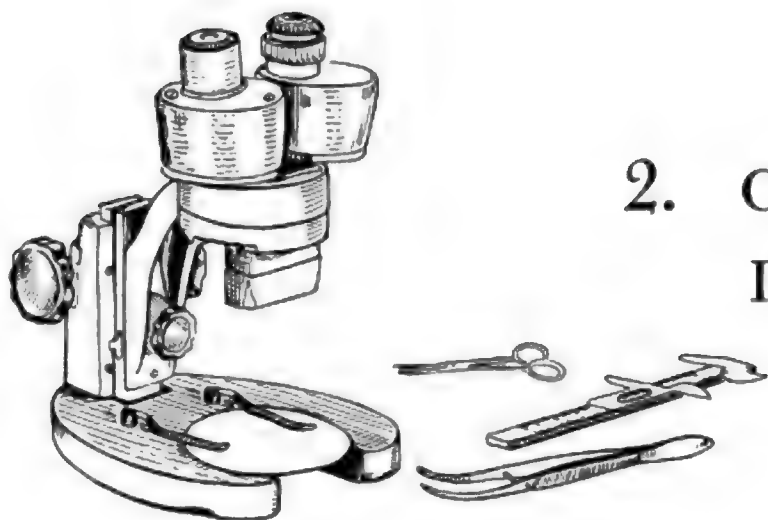
A traveller, wandering in the burning deserts of Africa, and fainting under the power of a vertical sun, who hears the roaring of a famished tiger furious for prey, and who has no means either of escape or defence, feels not greater dread than when, passing through the vast forest of the warm and humid regions of the New World, he scents the abominable feter of the *boiquira*<sup>13</sup> hears the terrifying noise of its portentous rattle, and observes it ready to spring upon him, from amid the verdant foliage and brilliant flowers of these delightful solitudes. . . . Here [in France] we have no dreadful serpent to infect with its mortal venom, the water, in which it swims with facility; the trees, whose boughs it glides over with agility; the earth, whose caverns it fills with its hideous form; the solitary woods where it exercises the same sanguinary sway as the tiger in its burning deserts, and in the obscurity of which its prey is more certainly exposed to its envenomed tooth. *Lacépède, 1788-89, vol. 2, pp. 390, 419; translation by Kerr, 1802, vol. 4, pp. 245, 277.*



The rattlesnake is among the most deadly enemies of all creatures. If he cannot swallow an animal he will bite it, and death is the penalty in both cases. *Buffalo Jones, frontiersman, quoted by Inman (1899, p. 179).*

In subsequent chapters we shall review the real character of the rattlesnake, the reptile to which Virginia Duncan (1945, p. 167) referred as "the snake without a friend."

<sup>13</sup> A name for the rattlesnake of South America.



## 2. Classification and Identification

### INTRODUCTION

Anyone having only a casual interest in rattlesnakes, particularly if concerned primarily with how and where they live, should skip this chapter or read only its introduction. To conform to a plan of logical development, it has been necessary to place this information on the classification and identification of the different kinds of rattlesnakes ahead of the more interesting material on their habits. Classification is necessarily technical, and a reader of this chapter, too early in his perusal of the book as a whole, might well be discouraged by these technicalities, and might leap to the conclusion that all sections of the book are equally specialized and complex. He will find, I hope, that such is not true. Therefore I suggest that, if he is a beginner in herpetology, he do little more than skim through the pages of this chapter, to learn only enough about its contents so that he will know where to find what he seeks, if he wishes subsequently to study the taxonomy of these creatures or to identify a particular specimen. I believe, however, that even the most desultory reader will find interest in the photographs of some of the different kinds of rattlesnakes and the maps that show where each kind is found.

The notable differences and variations that exist among the rattlesnakes—differences in size, color and pattern, habits and habitats—are discussed in other chapters of this book. Characteristics and features observed in one species of rattler are not necessarily found in others. Even in such an important practical matter as the danger inherent in rattlesnake bite, generalities are of little value, because differences in rattlesnake size and venom potency will materially affect the outcome.

To anyone having even a superficial interest in rattlesnakes, an ability to distinguish between the several kinds would naturally be the first subject of inquiry. Elsewhere I have given some data on colors and patterns, and on the peculiarities of scalation that characterize some forms of rattlesnakes. But to identify a particular snake requires the application of certain methods of recognition; it would not be feasible to read a succession of descriptions and select the one best fitting

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the specimen at hand. It is true that in some areas, where only one species is to be found, the classification can be based on geography, but this is not usually the case.

A schedule calling attention, successively, to the particular characters in which the several species differ is called a key. The purpose of a key is to offer the user a series of alternative courses, which, if accurately selected, will ultimately designate the particular subspecies to which any individual snake being identified belongs. However, before presenting such keys, I deem it necessary to touch on certain matters of nomenclature and taxonomy.

When this book was originally begun in 1945, it was to have been of limited scope—it was not expected to go beyond the habits of the western rattlesnake (*Crotalus viridis*) and its several subspecies. At that time I hoped that technical terms—including the use of the technical names of the snakes themselves—could be minimized. However, as the work was expanded, I found it increasingly difficult, if clarity and accuracy were to be retained, to adhere to this program. And when it comes to the identification of rattlesnakes, technical terms are essential. Superficially—in pattern and color particularly—some rattlesnakes are more like individuals of other subspecies than they are like fellow members of their own subspecies from other areas. For example, the Mojave rattlesnakes (*C. s. scutulatus*) of the Antelope Valley and the western Mojave Desert in California look more like the northern Pacific rattlers (*C. v. oreganus*) of the southern San Joaquin Valley than they resemble the Mojave rattlers of the mountains of central Arizona; similarly, the San Joaquin Valley snakes look more like the Mojave rattlers than they do like their own relatives—that is, other northern Pacifics—from the nearby Sierra Nevada. But the true relationships are quickly disclosed by noting certain differences in squamation (scale numbers and arrangements) between Mojave and northern Pacific rattlers. These scale differences are in no way conspicuous, and technical terms must be employed in connection with their use in keys.

Elsewhere (p. 23) I have explained why it has been necessary, for the sake of clarity and consistency, to utilize technical (Latin) names for the several rattlesnake species and subspecies. This is especially true in the present chapter on classification and identification, where definiteness and brevity are essential.

The data presented in this taxonomic section include the following parts:

- A check list setting forth, by subspecies, the technical and vernacular names of all the subspecies now recognized; also, an abbreviated synonymy (a sort of historical summary of the technical names that have been suggested for the subspecies) and the geographical range of each subspecies.

- A condensed, alphabetically arranged synonymy giving the present status of each technical name; and (separately) an alphabetical index from which the technical name applicable to any common name may be ascertained.

- A set of illustrated keys to the rattlesnakes, segregated into several geographical areas, prefaced by a suitable glossary.

- Geographic distribution tables (by states, provinces, and so on) segregated into the same geographical divisions as the keys.

- Tables showing the numerical ranges of certain characters of each subspecies.

Only general geographical ranges can be given, whether in the check list, the geographical tables that accompany the keys, or the maps. Rarely is any kind of rattlesnake found uniformly distributed throughout an area, for these snakes are much affected by ecological conditions. Some are restricted to the higher

mountains, others to rocky foothills or plains. Some kinds have been largely or entirely exterminated about cities or in areas of intensive agricultural development that they once occupied. So these range delineations are intended to outline the territories within which a subspecies occurs, but not necessarily, or even usually, are they to be expected everywhere within that boundary.

## A CHECK LIST OF THE RATTLESNAKES<sup>1</sup>

This check list of existing rattlesnakes is arranged alphabetically by species under each of the two genera, with the subspecies in alphabetical order under each species, except that the type or nominate subspecies is given first.

No attempt has been made to compile a complete synonymy. The following entries are made, to the extent applicable, under each form:

The technical name as recognized at this time

The recommended vernacular name

The earliest mention of the form under consideration, based on an allocation to the territory it is now known to occupy

Subsequent designations of the form under names applied prior to the name now recognized, if such names were generally accepted

The earliest mention of the name now accepted, in its originally cited form, with type locality and type specimen

The earliest citation of each synonym or homonym in its originally cited form, with type locality and type specimen

The earliest allocation to the proper genus if originally assigned to another

The first citation of the name as presently recognized. If two citations of the same name are given, the second represents either a broader or more restricted coverage.

The geographical range of each subspecies. These are given only in general terms. Ranges may be, and often are, quite discontinuous, depending on local ecological conditions. Thus scattered colonies, rather than uniformly distributed populations, are of frequent occurrence.

To find the present allocation or status of any technical name, whether or not valid, consult the condensed alphabetical synonymy, p. 101. To find the technical name corresponding to any common name see p. 104.

Only such of the references cited as have other than taxonomic interest are included in the general bibliography at the end of the book, since students interested in nomenclature will readily recognize the references in the abbreviated form of the citations in this check list.

Minor emendations—for example, the substitution of *terrificus* for *terrifica*, or *oregonus* for *oreganus*—are not recognized by separate entries. If a subsequent author has allocated a name to a species or subspecies not contemplated by the original describer, such transfer is not recognized in the synonymy of the substituted species. For example, the application of the name *concolor* to *tigris* is not

<sup>1</sup> The following are the major changes in this check list as compared with that published in the first edition of this book. New species added: *Crotalus lannomi* Tanner, 1966. *Crotalus vegrandis* is now considered a full species, not a subspecies of *C. durissus*. New subspecies added: *Crotalus mitchellii angelensis* Klauber, 1963; *Crotalus willardi amabilis* Anderson, 1962. Re-established subspecies added: *Crotalus intermedius gloydi* Taylor, 1941; *Crotalus viridis concolor* Woodbury, 1929 (replacing *Crotalus viridis decolor* Klauber, 1930); and *Sistrurus catenatus edwardsii* Baird and Girard, 1853.

recognized by an entry in the synonymy, for this name was originally intended to describe a subspecies quite distinct from *tigris*.

If a name as originally used was clearly composite—for example, *C. boquiria* Lacépède, 1789—it has been entered only under the present species most strongly indicated, in this example as a synonym of *horridus*, rather than under both *horridus* and *terrificus*. Often such allocations are based in part upon the usages of subsequent authors.

If real doubt remains as to the proper applicability of certain names—for example, *horridus*, *durissus*, and *terrificus*—I have followed the assignments in general use during the past twenty-five years.

The validation of *nomina nuda* as synonyms are traced by appropriate footnotes. Secondary homonyms, involving the temporary and inaccurate assignment of a nonrattlesnake to the genera *Sistrurus* and *Crotalus*, or of a rattlesnake to some other genus, have rarely occurred, probably because of the conspicuous character of the rattle itself. However, future authors would do well to avoid describing new rattlers under such names as *orientalis* and *piscivorus*.

I have been somewhat inconsistent in the treatment of island forms. Many taxonomists adhere to the strictly objective and easily applied rule that a subspecific designation must involve the actuality, or at least the possibility, of existing intergradation, which most island forms clearly lack. But consistently to apply this rule causes a loss in the value of nomenclature, insofar as the latter can indicate relationships. Thus, for example, if the island form *estebanensis* is considered a full species, its name will indicate no closer relationship to *molossus* than to *atrox* or *mitchellii*. Yet its derivation from *molossus* is so evident, and the extent of its morphological divergence from *molossus molossus* so moderate, that the adoption of the subspecific name *C. molossus estebanensis* has a real practical value. So, in assigning the names of island subspecies, I have been guided, not by the possibility of intergradation, of which clearly there is none, but by the extent of the divergence from the corresponding mainland form. This explains my recognition of *tortugensis* and *exsul* as full species in spite of their obvious relationships to *atrox* and *ruber*, respectively. The latter is admittedly a borderline case; future authors may prefer the names *C. exsul ruber* and *C. exsul lucasensis* for the mainland forms (*exsul* being an older name than *ruber*). The divergence of *tortugensis* from *atrox* seems wider than that of *exsul* from *ruber*.

In the case of some Mexican and other mainland forms, of which adequate collections are not at hand, I have adopted subspecific relationships where such are indicated, even though the lack of specimens from critical intermediate areas leaves intergradation unproved. Again, this has been done for the purpose of indicating probable relationships.

#### ABBREVIATIONS USED IN THE DESIGNATION OF TYPE SPECIMENS

BM	British Museum (Natural History), London
Bremen	Naturhistorischen Museums, Bremen
BYU	Brigham Young University, Provo
CAS	California Academy of Sciences, San Francisco
Chi.Acad.	Chicago Academy of Sciences
CM	Carnegie Museum, Pittsburgh

CNHM	Chicago Natural History Museum (formerly Field Museum)
EHT-HMS	Private collection of E. H. Taylor and H. M. Smith
Leyden Mus.	Rijksmuseum van Natuurlijke Historie, Leiden
LMK	Private collection of L. M. Klauber, San Diego, now transferred to SDSNH
MCZ	Museum of Comparative Zoölogy, Harvard University
Milan	Museo Civico di Storia Naturale, Milan
MVZ	Museum of Vertebrate Zoölogy, University of California, Berkeley
MZUM	Museum of Zoölogy, University of Michigan, Ann Arbor
PANS	Academy of Natural Sciences of Philadelphia
SDSNH	Natural History Museum, San Diego Society of Natural History
Stanford	Natural History Museum, Stanford University, now transferred to CAS
Taylor	Private collection of E. H. Taylor
USNM	United States National Museum, Washington
Utah	University of Utah, Salt Lake City

### Genus *Crotalus* Linné

1758. *Crotalus* Linné, Syst. Nat., ed. 10, p. 214. Type *horridus*, confirmed by Opinion 92, Int. Comm. Zoöl. Nomen. See also Direction 56, p. 356, 1956, and Direction 57, p. 374, Opinions and Orders, vol. 1.
1764. *Crotalophorus* Houttuyn, Natuur. Hist., vol. 6, part 1, p. 290. Type *horridus*.
1768. *Caudisona* Laurenti, Synops. Rept., p. 92. Type *terrificus*, by page priority.
1818. *Crotalinus* Rafinesque, Amer. Month. Mag. & Crit. Rev., vol. 3, no. 6, p. 416. Type *cyanurus* (= *horridus*).
1820. *Crotalurus* Rafinesque, Annals of Nature, no. 1, p. 5. Type *catenatus*.
1830. *Uropsophus* Wagler, Nat. Syst. Amph., p. 176. Type *triseriatus*.
1843. *Urocrotalon* Fitzinger, Syst. Rept., p. 29. Type *durissus*.
1866. *Aploaspis* Cope, Proc. Acad. Nat. Sci. Phila., vol. 18, no. 4, p. 310. Type *lepida* (= *lepidus*).
1875. *Aechmophrys* Coues, Rept. Explor. & Surv. W. of 100th Mer. (Wheeler), vol. 5, chap. 5, p. 609. Type *cerastes*.
1883. *Haploaspis* Cope, Proc. Acad. Nat. Sci. Phila., vol. 35, part 1, p. 13 (emendation of *Aploaspis*, 1866).
1930. *Paracrotalus* Reuss, Glasnik Zem. Muz., Sarajevo, vol. 42, p. 88. Type *terrificus*.

### *Crotalus adamanteus* Beauvois

#### Eastern Diamondback Rattlesnake

#### Fig. 2:11

1799. *Crotalus adamanteus* Beauvois, Trans. Amer. Philos. Soc., vol. 4, no. 42, p. 368. Type locality: U. S.; type specimen: none designated. Type locality: restricted to Charleston, S. C. by Schmidt, 1953, p. 227.
1802. *Crotalus rhombifer* Latreille, in Sonnini and Latreille, Hist. Nat. Rept., vol. 3, p. 197. Type locality: southern U. S.; type specimen: none designated.
1805. *Crotalus rhombiferus* Brickell, Phila. Med. & Phys. Jour., vol. 2, part 1, sec. 3, p. 164 (not of Latreille, 1802). Type locality: not stated, probably vicinity of Savannah, Georgia; type specimen: none designated.
1858. *Crotalus adamanteus* var. *adamanteus* Jan, Rev. Mag. Zoöl., ser. 2, vol. 10, p. 153 (Prod. Icon. Desc. Ophid., p. 28).
1895. *Crotalus adamanteus* Stejneger, Rept. U. S. Nat. Mus. for 1893, p. 433.

*Range*:—The coastal plains of the following Southeastern and Gulf states: North Carolina south of Albemarle Sound; South Carolina; Georgia; all of Florida, with many of the adjacent keys; Alabama; Mississippi; and southeastern Louisiana. A lowland species (fig. 2:1).

***Crotalus atrox* Baird and Girard**  
**Western Diamondback Rattlesnake**  
**Fig. 2:12**

1852. *Crotalus cinereus*<sup>2</sup> Le Conte, in Hallowell, Proc. Acad. Nat. Sci. Phila., vol. 6, p. 177. Type locality: near the Colorado [River]; type specimen: described, but disposition unknown.
1853. *Crotalus atrox* Baird and Girard, Cat. North Amer. Rept., part 1, p. 5. Type locality: Indianola [Calhoun County], Texas; type specimen: USNM 7761.
1858. *Crotalus adamanteus* var. *atrox* Jan, Rev. Mag. Zool., ser. 2, vol. 10, p. 153 (Prod. Icon. Desc. Ophid., p. 28).
1861. *Caudisona atrox* var. *atrox* Kennicott, Proc. Acad. Nat. Sci. Phila., vol. 13, p. 206.
1861. *Caudisona atrox* var. *sonoraensis* Kennicott, Proc. Acad. Nat. Sci. Phila., vol. 13, p. 206. Type locality: Sonora and vicinity; type specimen: none designated.
1930. *Crotalus atrox* Klauber, Bull. Zool. Soc. San Diego, no. 6, p. 6.

*Range*:—From Arkansas and Oklahoma south to central Mexico and west to California, including the following: central and west-central Arkansas; extreme southeastern and southwestern Missouri (somewhat doubtful); extreme southeastern Kansas; central and southern Oklahoma; Texas west of long. 95°, including various coastal islands; New Mexico south of lat. 36°, but not including the west-central mountains; Arizona south and west of the line Ash Fork–Clifton; the southern tip of Nevada; the lowland desert areas of Riverside and Imperial counties, California; extreme northeastern Baja California; and the Mexican states of Sonora, extreme northern Sinaloa, Chihuahua, Durango, Zacatecas, Coahuila, Nuevo León, Tamaulipas, San Luis Potosí, and northern Veracruz; isolated colonies in central Veracruz and southeastern Oaxaca; possibly present in Hidalgo. Also Tiburón, Turner, San Pedro Mártir, Santa Cruz, and Santa María (Sinaloa) islands in the Gulf of California (fig. 2:1).

***Crotalus basiliscus basiliscus* (Cope)**  
**Mexican West-Coast Rattlesnake**  
**Fig. 2:13**

1864. *Caudisona basilisca* Cope, Proc. Acad. Nat. Sci. Phila., vol. 16, no. 3, p. 166. Type locality: near Colima, Colima, Mexico; type specimen: Smithsonian 6118, now USNM 53586. Type locality subsequently restricted to Colima, Colima, by Smith and Taylor, 1950, Univ. Kans. Sci. Bull., vol. 33, part 2, no. 8, p. 328.
1875. *Crotalus basiliscus* Cope, in Yarrow, Surv. W. of 100th Merid. (Wheeler), vol. 5, chap. 4, p. 532.
1896. *Crotalus terrificus* (part) Boulenger, Cat. Snakes Brit. Mus., vol. 3, p. 573.
1929. *Crotalus terrificus basiliscus* Amaral, Bull. Antivenin Inst. Amer., vol. 3, no. 1, p. 5.
1948. *Crotalus basiliscus basiliscus* Gloyd, Nat. Hist. Misc., no. 17, p. 1.

*Range*:—From extreme southern Sonora, southeasterly along the west coast of Mexico, including: Sinaloa, Navarrit, Jalisco, Colima, and western Michoacán (fig. 2:2).

***Crotalus basiliscus oaxacus* Gloyd**  
**Oaxacan Rattlesnake**  
**Fig. 2:14**

1936. *Crotalus basiliscus* (part) Klauber, Trans. San Diego Soc. Nat. Hist., vol. 8, no. 20, p. 249, table 1 (footnote).
1948. *Crotalus basiliscus oaxacus* Gloyd, Nat. Hist., Misc., no. 17, p. 1. Type locality: Oaxaca, Oaxaca, Mexico; type specimen: USNM 46467.

*Range*:—Known only from central Oaxaca, Mexico (fig. 2:2).

<sup>2</sup> In my judgment *C. cinereus*, rather than *C. atrox*, was once the proper name for the western diamond rattlesnake. However, the International Commission on Zoological Nomenclature, in the interest of conserving widely used names, established *atrox* as the accepted name for this snake and suppressed *cinereus* (Opinion 365, Nov. 16, 1955).

***Crotalus catalinensis* Cliff**

**Santa Catalina Island Rattlesnake; Rattleless Rattlesnake<sup>a</sup>**

Fig. 2:15

1954. *Crotalus catalinensis* Cliff, Trans. San Diego Soc. Nat. Hist., vol. 12, no. 5, p. 80. Type locality: Santa Catalina Island, Gulf of California, Mexico; type specimen: Stanford 15631.

*Range*.—Found only on Santa Catalina Island. This Mexican island should not be confused with the American island of the same name off the coast of California (fig. 2:9).

***Crotalus cerastes cerastes* Hallowell**

**Mojave Desert Sidewinder**

Fig. 2:16

1854. *Crotalus cerastes* Hallowell, Proc. Acad. Nat. Sci. Phila., vol. 7, p. 95. Type locality: borders of the Mohave River, and in the desert of the Mohave [California]; type specimen: designated, but not by number, disposition unknown, but probably was USNM 352, now PANS 7098.

1944. *Crotalus cerastes cerastes* Klauber, Trans. San Diego Soc. Nat. Hist., vol. 10, no. 8, p. 94.

*Range*.—The desert regions of eastern (but not extreme southeastern) California, southern Nevada, southwestern Utah, and northwestern Arizona, including the following: extreme southern Mono, Inyo, eastern Kern, northeastern Los Angeles, and San Bernardino counties in California; southeastern Esmeralda, southern Nye, extreme southern Lincoln, and Clark counties in Nevada; southwestern and central Washington County, Utah; and extreme northwestern and west-central Mohave County, Arizona (fig. 2:3).

***Crotalus cerastes cercobombus* Savage and Cliff**

**Sonoran Desert Sidewinder**

Fig. 2:17

1895. *Crotalus cerastes* (part) Stejneger, Rept. U. S. Nat. Mus. for 1893, p. 451.

1944. *Crotalus cerastes laterorepens* (part) Klauber, Trans. San Diego Soc. Nat. Hist., vol. 10, no. 8, p. 94.

1953. *Crotalus cerastes cercobombus* Savage and Cliff, Nat. Hist. Misc., no. 119, p. 2. Type locality: Near Gila Bend, Maricopa County, Arizona; type specimen: Stanford 7287.

<sup>a</sup> The acquisition of 12 additional specimens of *Crotalus catalinensis*, all but two of which, like the type, are without loose rattles, but have only the rattle that covers the matrix, and, further, have such shallow grooves in the matrix that loose rattles could not ordinarily be retained, indicates that this is usually characteristic of the species. I have therefore given this snake the alternative common names of Santa Catalina Island rattlesnake and rattleless rattlesnake and have used this character in the appropriate key, resulting in some simplification. The head scales of *catalinensis*, especially the postnasal-preocular contact, and the scales in the prefrontal area, indicate a closer relationship with *C. scutulatus* than with *C. atrox* as previously supposed. The pattern also resembles that of *scutulatus*, although the postocular light stripe intersects the mouth, as in *atrox*. The light borders of the diamonds are unicolor as in *scutulatus*; also the dark tail rings are narrower than the interspaces, a *scutulatus* characteristic. The rattle matrix is dark above and light below as in *scutulatus*. These and other characteristics suggest that the original colonizers of this island were probably *C. scutulatus*. The deterioration of the rattle is not to be explained by the usual slow process of evolution through natural selection. It is doubtful that there has been a difference in use of the rattle by the snakes of this island, as compared with the species or subspecies of rattlesnakes that have colonized other islands in the Gulf of California, all of which have retained fully functional rattles. Rather we may presume that one or more of the original colonists on Santa Catalina Island had defective rattles and that this characteristic persisted in the progeny, producing a fixed mutation. The defect is such, owing to the configuration of the matrix and the pliability of the newly formed rattle, that successive rattle lobes are shed with the skin and are not retained, as is normal in rattlesnakes. Occasionally the button may be retained for one shedding.

## 34 *Classification and Identification*

*Range*.—Eastern Yuma, southern Maricopa, western Pinal, and western Pima counties in Arizona; and northwestern Sonora, Mexico, except that part of the state north and west of Bahia Adair. Also Tiburón Island (fig. 2:3).

### ***Crotalus cerastes laterorepens* Klauber**

#### **Colorado Desert Sidewinder**

Fig. 2:18

1859. *Crotalus cerastes* (part) Hallowell, Pac. R.R. Surv. Rept. (Williamson), vol. 10, part 4, p. 17.

1944. *Crotalus cerastes laterorepens* Klauber, Trans. San Diego Soc. Nat. Hist., vol. 10, no. 8, p. 94.

Type locality: The Narrows, San Diego County, California; type specimen: LMK 34074.

*Range*.—The desert areas of central and eastern Riverside, northeastern San Diego, and Imperial counties in California; western Yuma County, Arizona; northeastern Baja California, and extreme northwestern Sonora, Mexico (fig. 2:3).

### ***Crotalus durissus durissus* Linné**

#### **Central American Rattlesnake**

Fig. 2:19

1758. *Crotalus durissus* Linné, Syst. Nat., ed. 10, p. 214. Type locality: America; type specimen: originally in the Claudius Grill Surinam collection; later the collection was sent to the Zoölogical Museum of the Royal University at Upsala, Sweden, but this type is lost.<sup>4</sup> Type locality subsequently restricted to Jalapa, Veracruz, Mexico, by Smith and Taylor, Univ. Kans. Sci. Bull., vol. 33, part 2, no. 8, p. 348, 1950.

1802. *Crotalus simus* Latreille, in Sonnini and Latreille, Hist. Nat. Rept., vol. 3, p. 202; vol. 4, p. 323. Type locality: Ceylon (in error, following Seba); type specimen, not designated.

1867. *Crotalus terrificus* (part) Cope, Proc. Acad. Nat. Sci. Phila., vol. 18, no. 4, p. 308.

1905. ?*Crotalus pulvis* Ditmars, Ninth Ann. Rept. N. Y. Zoöl. Soc., p. 199. Type locality: 20 miles inland from Managua, Nicaragua; type specimen: MCZ 7044, possibly an albino *durissus*, although almost certainly a specimen of *Crotalus unicolor* from Aruba Island.

1929. *Crotalus terrificus durissus* (part) Amaral, Bull. Antivenin Inst. Amer., vol. 3, no. 1, p. 5.

1936. *Crotalus durissus durissus* Klauber, Occ. Papers San Diego Soc. Nat. Hist., no. 1, p. 4.

1937. *Crotalus terrificus copeanus*<sup>5</sup> Amaral, Mem. Inst. Butantan, vol. 10, p. 161. Type locality: Central America; type specimen: none designated.

1952. *Crotalus durissus durissus* Klauber, Bull. Zoöl. Soc. San Diego, no. 26, p. 61.

*Range*.—Southeastern Mexico and Central America including: central Veracruz, southeastern Oaxaca, Tabasco, and Chiapas in Mexico; central and southern Guatemala, western and southern Honduras, southern British Honduras, El Salvador, southwestern Nicaragua, and northwestern and central Costa Rica (fig. 2:4).

### ***Crotalus durissus culminatus* Klauber**

#### **Northwestern Neotropical Rattlesnake**

Fig. 2:20

1895. *Crotalus horridus* (part) Günther, Biol. Cent.-Amer., Reptilia and Batrachia, p. 194. (Not *C. horridus* of authors.)

<sup>4</sup> The uncertainties regarding the proper application of the Linnean names to rattlesnakes have been discussed by Klauber, Bull. Zoöl. Soc. San Diego, no. 17, pp. 81–95, 1941; Copeia, no. 1, of 1948, pp. 1–3. For many years during the nineteenth century, the Neotropical (Central and South American) rattler was often referred to as *C. horridus*, and the timber rattler of the eastern United States as *C. durissus*. To avoid confusion I have ignored these allocations in this check list, since in present usage the allocation of these names is reversed.

<sup>5</sup> Although a *nomen nudum* for technical reasons (Rules Zoöl. Nomen., 1926, art. 25,c), the name was intended as a substitute for *C. d. durissus* (see Klauber, 1941, p. 91). Gloyd (1940, p. 123) has established *copeanus* as a synonym of *durissus* by introduction of the name into the synonymy of that subspecies.

1896. *Crotalus terrificus* (part) Boulenger, Cat. Snakes Brit. Mus., vol. 3, p. 573.  
 1935. *Crotalus terrificus basiliscus* (part) Martín del Campo, Anales Inst. Biol., vol. 6, nos. 3 and 4, p. 296.  
 1936. *Crotalus durissus durissus* (part) Klauber, Trans. San Diego Soc. Nat. Hist., vol. 8, no. 20, pp. 190, 233.  
 1952. *Crotalus durissus culminatus* Klauber, Bull. Zoöl. Soc. San Diego, no. 26, p. 65. Type locality: Hacienda El Sabino, near Uruapan, Michoacán, Mexico; type specimen: Taylor 5224.  
 Range:—Southwestern Michoacán, southern and western Morelos, Guerrero, and southwestern Oaxaca, Mexico; probably extreme western Puebla, and possibly Distrito Federal (fig. 2:4).

***Crotalus durissus terrificus*<sup>†</sup> (Laurenti)**

**South American Rattlesnake**

**Figs. 2:21 and 2:22**

1758. *Crotalus dryinas*<sup>‡</sup> Linné, Syst. Nat., ed. 10, p. 214. Type locality: America; type specimen: originally in the Adolph Frideric Museum; later this collection was sent to the Zoölogical Museum of the Royal University at Upsala, Sweden, but this type is lost.

\* A. R. Hoge, in 1966, Mem. Inst. Butantan, vol. 32, pp. 137–148, divided the South American rattlesnake subspecies, which I have herein considered to belong to the single subspecies *Crotalus durissus terrificus*, into a total of 8 subspecies, including the two, *C. d. durissus* (in North America) and *C. d. terrificus*, that I have recognized. It appears to me that Hoge's work is not sufficiently complete and detailed to permit the segregation and differentiation of these 8 subspecies and therefore I have not deemed it advisable to give them full recognition and acceptance for inclusion in the list of species contained in chapter 1, or in the checklist, synonymies, maps, and keys contained in chapter 2. As a partial substitute, and in order that this edition will not be completely lacking in the presentation of Hoge's work, I offer herewith, in the form of a footnote, an abbreviated checklist of Hoge's South American subspecies of *Crotalus durissus*, with the exception of *C. unicolor* and *C. vegrandis*, which I consider full species.

In the checklist that follows I mention only the name of the original describer, since I do not always concur with Hoge's nomenclatorial derivations.

The following is an abbreviated reference list of the South American rattlesnake subspecies that Hoge recognizes:

*Crotalus durissus durissus* Linnaeus, 1758, Syst. Nat., 10th ed., vol. 1, p. 214. Type Locality: Jalapa, Veracruz, Mexico. Range: Southern Mexico, Central America, Colombia, and Venezuela.

*Crotalus durissus cascavella*, Wagler, 1824, in Spix, Serp. Bras., p. 60. Neotype: IBH 23,400, Mina Caraiba, Bahia, Brazil. Range: the dry "caatinga" regions of the Brazilian states of Maranhão, Ceará, Piauí, Pernambuco, Alagoas, Rio Grande do Norte, Paraíba, Bahia, and Minas Gerais.

*Crotalus durissus collineatus* Amaral, 1926, Rev. Mus. Paulista, vol. 15, p. 90. Lectotype: IBH, 2180, State of Mato Grosso, Brazil. Range: Sw. Mato Grosso, Goiás, Federal District, Minas Gerais, Ne. São Paulo, and Nw. Paraná, Brazil.

*Crotalus durissus cumanensis* Humboldt, 1833, Rec. d'Obs. Zool., vol. 2, p. 6. Type locality: Cumaná, Venezuela. Range: Venezuela except high Andes, and except the savannas of Monagas, Bolívar, and Amazonas.

*Crotalus durissus dryinas* Linnaeus, 1758, Syst. Nat., 10th ed., vol. 1, p. 214. Type locality: Paramaribo, Surinam. Range: The Guianas.

*Crotalus durissus marajoensis* Hoge, 1965, Mem. Inst. Butantan, vol. 32, p. 143. Type specimen: IBH 17779, Tuiuiú, Marajó Island, State of Pará, Brazil. Range: Marajó Island, State of Pará, Brazil.

*Crotalus durissus ruruima* Hoge, 1965, Mem. Inst. Butantan, vol. 32, p. 145. Type specimen AMNH 36056, Paulo Camp, Mt. Roraima, Venezuela. Range: Brazilian-Venezuelan border, vicinity of Mt. Roraima.

*Crotalus durissus terrificus* (Laurenti), 1768, Syn. Rept., p. 93. Neotype: IBH 22997, Julio de Castilho, Taquari, State of Rio Grande do Sul, Brazil. Range: States of Minas Gerais, São Paulo, Paraná, Santa Catarina, and Rio Grande do Sul, Brazil, south to the limits of the rattlesnake range in northern Argentina.

<sup>‡</sup> The reasons for not adopting this name, despite the fact that the type probably did represent the South American rattlesnake, and that the name has priority over *terrificus*, have been discussed by Klauber, Bull. Zoöl. Soc. San Diego, no. 17, pp. 81–95, 1941; Copeia, no. 1 of 1948, pp. 1–3. If the type of *dryinas* is ever found, so that the propriety of this name for the South

1768. *Caudisona terrifica* Laurenti, Synopsis Rept., p. 93. Type locality: America below lat. 45° N.; type specimen: none designated.
1778. *Crotalus exalbidus* Boddaert, Nov. Act. Phys.-Med. Acad. Caes. Leop.-Carol., vol. 7, no. 2, p. 16. Type locality: not given; type specimen: none designated.
1790. *Crotalus durissus* Bonnaterre, Encycl. Meth.: Ophiologie, p. 2.
1802. *Crotalus immaculatus* Latreille, in Sonnini and Latreille, Hist. Nat. Rept., vol. 3, p. 201; vol. 4, p. 323. Type locality: East Indies (in error, following Seba); type specimen: none designated.
1803. *Crotalus strepitans* Daudin, Hist. Nat. Rept., vol. 5, p. 318. Type locality: America; type specimen: none designated.
1824. *Crotalus cascavella* Wagler, in Spix, Serp. Bras. Spec. Nov., p. 60. Type locality: province of Bahia, Brazil; type specimen: none designated.
1833. *Crotalus cumanensis* Humboldt, in Humboldt and Bonpland, Recueil d'Obs. Zool. Anat. Comp., vol. 2, p. 6. Type locality: Cumaná, Venezuela; type specimen: none designated.
1833. *Crotalus loeflingi* Humboldt, in Humboldt and Bonpland, Recueil d'Obs. Zool. Anat. Comp., vol. 2, p. 6. Type locality: Cumaná, Venezuela; type specimen: none designated.
1875. *Crotalus terrificus* Cope, in Yarrow, Surv. W. of 100th Merid. (Wheeler), vol. 5, chap. 4, p. 532.
1926. *Crotalus terrificus* var. *terrificus* Amaral, Revista Mus. Paulista, vol. 15, p. 90.
1926. *Crotalus terrificus* var. *collirhombeatus* Amaral, Revista Mus. Paulista, vol. 15, p. 90. Type locality: northeastern Brazil; type specimen: none designated.
1926. *Crotalus terrificus* var. *collilineatus* Amaral, Revista Mus. Paulista, vol. 15, p. 90. Type localities: central, southeastern, and southern Brazil, Argentina, Paraguay, and probably Uruguay and Bolivia; type specimen: none designated.
1929. *Crotalus terrificus durissus* (part) Amaral, Bull. Antivenin Inst. Amer., vol. 3, no. 1, p. 5.
1930. *Paracrotalus terrificus* Reuss, Glasnik Zem. Muz., Sarajevo, vol. 42, p. 88.
1936. *Crotalus durissus terrificus* Klauber, Occ. Papers, San Diego Soc. Nat. Hist., no. 1, p. 4.
1956. *Crotalus terrificus crotaminicus* Moura Gonçalves, Anais Acad. Brasil Cienc., vol. 28, no. 3, p. 365. Type localities: Morro Agudo, Franca, Ituverava, Sao Paulo, Brazil; type specimen: none designated.\*

*Range*.—South America, including: northern and central Colombia, Venezuela, British Guiana, Surinam, French Guiana, Brazil, southeastern Peru, eastern Bolivia, Paraguay, Uruguay, and northern Argentina. May occur in eastern (trans-Andean) Ecuador; there is uncertainty as to its occurrence in the upper Amazon basin (fig. 2:5).

American rattlesnake could be established, then, in the interest of nomenclatorial stability, an application should be made to the International Commission on Zoölogical Nomenclature for the retention of *terrificus* as the *subspecific* name for the South American rattler. This procedure is not applicable to validate *terrificus* as the *specific* name for this snake—a current usage of many South American herpetologists—as long as the Central and South American snakes are deemed conspecific, for *durissus* is the older name. Only if we segregate these forms into separate species—by reason of the Panamanian gap in their ranges—could the South American snake become *Crotalus terrificus*. Unfortunately the rattlesnakes of Venezuela and Colombia are, in some characteristics, more like the snakes of Central America than they are like the rattlers of southern Brazil, so that this segregation does not seem proper, and the rattlesnakes of South America should be designated *Crotalus durissus terrificus*. I have no doubt that, when sufficient material becomes available for study, at least three South American subspecies of *durissus* will be recognized: *C. durissus cumanensis* Humboldt, 1833, in the north; *C. durissus cascavella* Wagler, 1824, in the Brazilian “bulge”; and *C. durissus terrificus* Laurenti, 1768, in the south. These further subdivisions will be useful in venom studies. I did not make these segregations in this book because I was unable to secure sufficient material wherewith to determine accurately either the territorial limits or character distinctions that would be necessary to define the three subspecies. See also footnote 6, above.

\* A biological subspecies; a *nomen nudum* since neither the description nor the differentiation from other subspecies complies with the requirements of the rules of the International Commission on Zoölogical Nomenclature. (article 13, a, i; article 45, b; article 73, recommendation 73A.) If the segregation is warranted (it is based on venom components), and the subspecies is re-described to conform to the Code, one of the older names (*cascavella*, Wagler, 1824; *cumanensis* or *loeflingi*, Humboldt, 1833; *collirhombeatus* or *collilineatus*, Amaral, 1926) might be found to take precedence over *crotaminicus*, if the type locality of any of these five falls within the range of *crotaminicus*.

***Crotalus durissus totonacus* Gloyd and Kauffeld**

**Totonacan Rattlesnake**

**Fig. 2:23**

1940. *Crotalus totonacus* Gloyd and Kauffeld, Bull. Chicago Acad. Sci., vol. 6, no. 2, p. 12. Type locality: Panaco Island, about 75 miles south of Tampico, Veracruz, Mexico, 12 miles inland from Cabo Rojo; type specimen: Chi. Acad. 4469.  
 1945. *Crotalus durissus totonacus* Smith and Taylor, U. S. Nat. Mus., Bull. 187, p. 190.  
 1950. *Crotalus basiliscus totonacus* Taylor, Univ. Kans. Sci. Bull., vol. 33, part 2, no. 11, p. 453.

*Range*:—Southern Tamaulipas, southeastern San Luis Potosí, and northern Veracruz (fig. 2:4).

***Crotalus durissus tzabcan* Klauber**

**Yucatán Neotropical Rattlesnake**

**Fig. 2:24**

1887. *Crotalus durissus* (part) Cope, Bull. U. S. Nat. Mus., no. 32, p. 89.  
 1895. *Crotalus horridus* (part) Günther, Biol. Cent.-Amer., Reptilia and Batrachia, p. 194. (Not *C. horridus* of authors.)  
 1896. *Crotalus terrificus* (part) Boulenger, Cat. Snakes Brit. Mus., vol. 3, p. 573.  
 1935. *Crotalus terrificus durissus* (part) Martín del Campo, Ann. Inst. Biol., vol. 6, nos. 3 & 4, p. 296.  
 1936. *Crotalus durissus durissus* (part) Klauber, Trans. San Diego Soc. Nat. Hist., vol. 8, no. 20, p. 190.  
 1952. *Crotalus durissus tzabcan* Klauber, Bull. Zoöl. Soc. San Diego, no. 26, p. 71. Type locality: Kantunil, Yucatán, Mexico; type specimen: CNHM 36168.

*Range*:—Yucatán, Campeche, Quintana Roo, and eastern Tabasco, Mexico; northern Guatamala and northern British Honduras (fig. 2:4).

***Crotalus enyo enyo* (Cope)**

**Lower California Rattlesnake**

**Fig. 2:25**

1861. *Caudisona enyo* Cope, Proc. Acad. Nat. Sci. Phila., vol. 13, p. 203. Type locality: Lower California; type specimen: Xantus 4663, now PANS 7159.<sup>\*</sup>  
 1875. *Crotalus enyo* Cope, Bull. U. S. Nat. Mus., no. 1, p. 33.  
 1929. *Crotalus confluentus enyo* Amaral, Bull. Antivenin Inst. Amer., vol. 2, no. 4, p. 94.  
 1954. *Crotalus enyo enyo* Lowe and Norris, Trans. San Diego Soc. Nat. Hist., vol. 12, no. 4, p. 52.

*Range*:—Baja California, Mexico, from the vicinity of El Mármol (lat. 30°N.) south to Cape San Lucas. Also the following islands: Magdalena, Santa Margarita, Espíritu Santo, Partida (southerly), San Francisco, San José, and Carmen (fig. 2:3).

***Crotalus enyo cerralvensis* Cliff**

**Cerralvo Island Rattlesnake**

**Fig. 2:26**

1954. *Crotalus enyo cerralvensis* Cliff, Trans. San Diego Soc. Nat. Hist., vol. 12, no. 5, p. 82. Type locality: Cerralvo Island, Gulf of California, Mexico; type specimen: Stanford 14021.

*Range*:—Cerralvo Island, Gulf of California, Mexico (fig. 2:3).

<sup>\*</sup> This specimen was collected at Cape San Lucas, Baja California, which thereby should be considered the type locality of the species.

***Crotalus enyo furvus* Lowe and Norris**

**Rosario Rattlesnake**

**Figs. 2:27 and 2:28**

1954. *Crotalus enyo furvus* Lowe and Norris, Trans. San Diego Soc. Nat. Hist., vol. 12, no. 4, p. 52. Type locality: 10.9 miles north of El Rosario, Baja California del Norte, Mexico; type specimen: MVZ 55388.

*Range*:—Baja California del Norte, on the west coast, from the San Telmo River south to El Rosario (fig. 2:3).

***Crotalus exsul* Garman**

**Cedros Island Diamond Rattlesnake**

**Fig. 2:29**

1883. *Crotalus exsul* Garman, Mem. Mus. Comp. Zool., vol. 8, no. 3, p. 114. Type locality: Cedros Island, west coast of Baja California; cotype specimens: MCZ 652 (2 specimens).

*Range*:—Cedros (or Cerros) Island, Pacific coast of Baja California, Mexico (fig. 2:1).

***Crotalus horridus horridus* Linné**

**Timber Rattlesnake**

**Fig. 2:30**

1758. *Crotalus horridus*<sup>10</sup> Linné, Syst. Nat., ed. 10, p. 214. Type locality: America; type specimen: originally in the King Adolph Frideric collection; later sent to the Royal Zoölogical State Museum at Stockholm, but now lost. Type locality restricted to vicinity of New York City by Schmidt, 1953, p. 227.
1789. *Crotalus boiquira* Lacépède, Hist. Nat. Serp., vol. 2, pp. 130 (first section), 390. Type locality: the New World; type specimen: none designated.
1818. *Crotalinus cyanurus* Rafinesque, Amer. Month. Mag. & Crit. Rev., vol. 3, no. 6, p. 416; vol. 4, no. 1, p. 41. Type locality: the barrens of Kentucky; type specimen: none designated.
1820. *Crotalurus cyanurus* Rafinesque, Ann. Nat., no. 1, p. 5.
1859. *Crotalus durissus*<sup>11</sup> var. *concolor* Jan, Rev. et Mag. Zool., ser. 2, vol. 10, p. 153. Type locality: North America; type specimen in Munich Mus.<sup>12</sup>
1873. *Crotalus fasciatus* Higgins, Ophidians, p. 81. Type locality: U. S. of Colombia; type specimen: none designated.
1935. *Crotalus horridus horridus* Gloyd, Copeia, no. 4, p. 176.

*Range*:—The northeastern and north-central United States, including: all the Atlantic states from central Vermont and New Hampshire to southern Virginia (except Delaware); West Virginia; southern Ohio; Kentucky; the mountains of western North Carolina, northwestern South Carolina, northern Georgia, central and eastern Tennessee, and extreme northern Alabama; southern Indiana; western and southern Illinois (except the southern tip); southwestern Wisconsin; extreme southeastern Minnesota; eastern Iowa; Missouri (except the southeastern corner); extreme southeastern Nebraska; Kansas

<sup>10</sup> The uncertainties regarding the proper allocation of the Linnean names to the rattlesnake species have been discussed by Klauber, Bull. Zool. Soc. San Diego, no. 17, pp. 81-95, 1941; Copeia, no. 1 of 1948, pp. 1-3. *C. horridus* has been confirmed as the genotype of *Crotalus* by Opinion 92 of the International Commission on Zoölogical Nomenclature; see also Direction 57, 1956.

<sup>11</sup> Jan's *durissus* is the equivalent of what we now call *C. horridus*, and thus all his *durissus* subspecies must be referred to *horridus*. There was confusion in the application of the names *horridus* and *durissus* for more than a century.

<sup>12</sup> Jan's *concolor* was suppressed by the International Commission in Opinion 339, Mar. 17, 1955.

(east of long. 97°W.); the mountainous area of northwestern Arkansas; the eastern half of Oklahoma; northeastern Texas. Also the Niagara and Essex Peninsula areas of the Lake Erie shore of Ontario, Canada, although it may now be exterminated there. This rattlesnake, once indigenous to what are now the most populous areas of the United States, has largely been killed off in industrial and agricultural districts, but still persists in adjacent mountains and forests, where rocky or wooded retreats are available. Thus its present range is intermittent, for it has now been exterminated in many areas over which it once ranged, including extreme southwestern Maine and (probably) northern Delaware (fig. 2:6).

### *Crotalus horridus atricaudatus* Latreille

#### Canebrake Rattlesnake

Fig. 2:31

1790. *Crotalus horridus* (part) Bonnaterre, Encycl. Meth.; Ophiologie, p. 1.  
 1802. *Crotalus atricaudatus* Latreille,<sup>13</sup> in Sonnini and Latreille, Hist. Nat. Rept., vol. 3, p. 209. Type locality: Carolina; type specimen: none designated. Type locality restricted to Charleston, S. C., by Schmidt, 1953, p. 228.  
 1805. *Crotalus zetazomae* Brickell, Phila. Med. & Phys. Jour., vol. 2, part 1, sec. 3, p. 164. Type locality: not stated, probably vicinity of Savannah, Georgia; type specimen: none designated.  
 1820. *Crotalus catesbaei*<sup>14</sup> Hemprich, Grund. Natur., p. 387. Type locality: South America to Carolina; type specimen: none designated.  
 1859. *Crotalus durissus* var. *melanurus* Jan, Rev. et Mag. Zool., ser. 2, vol. 10, p. 153. Type locality: South Carolina; type specimen: in the Paris Museum. *Nomen nudum*.<sup>15</sup>  
 1863. *Crotalus durissus* var. *mexicana* Jan, Elenco Syst. Ofidi, p. 123. Type locality: Mexico, Texas; type specimen: in Leyden Museum. *Nomen nudum*.<sup>16</sup>  
 1935. *Crotalus horridus atricaudatus* Gloyd, Copeia, no. 4, p. 176.

*Range*.—The lowlands of the South Atlantic and Gulf states and the lower Mississippi Valley, including: extreme southeastern Virginia; eastern North Carolina; South Carolina; central and southern Georgia; Florida north of lat. 29°30'N.; central and southern Alabama; Mississippi; extreme western Kentucky and Tennessee; Louisiana; southern and eastern Arkansas; extreme southeastern Missouri and southern Illinois; and Texas east of long. 99°W. and north of lat. 28°N. (fig. 2:6).

### *Crotalus intermedius intermedius* Troschel

#### Totalcan Small-Headed Rattlesnake

Fig. 2:32

1865. *Crotalus intermedius* Troschel, in Müller, Reisen in den Vereinigten Staaten, Canada und Mexico, vol. 3, p. 613. Type locality: Mexico; type specimen: in Müller collection; later in the collection of the Zoölogical Institute at Bonn. Dr. Robert Mertens advised me on March 8, 1951, that this collection was destroyed in World War II.  
 1882. *Crotalus intermedius* Fischer (not of Troschel, 1865), Abh. Nat. Ver. Bremen, vol. 7, p. 230. Type locality: Mexico; type specimen: Bremen 435.  
 1896. *Crotalus triseriatus* (part) Boulenger, Cat. Snakes Brit. Mus., vol. 3, p. 581.  
 1936. *Crotalus triseriatus triseriatus* (part) Klauber, Trans. San Diego Soc. Nat. Hist., vol. 8, no. 20, p. 247.

<sup>13</sup> Although Bosc furnished the description, it was Latreille who supplied the name. Bosc was usually nonbinominal (see Bosc, 1803, pp. 555-557).

<sup>14</sup> Diesing, 1851, Syst. Helminth., vol. 2, p. 431, attributes the specific name *catesbyanum* to Fitzinger. I am unable to locate Fitzinger's use of this name. He did use the name *catesbaei* (Neue Class. Rept., 1826, p. 63), but credited it to Hemprich, 1820.

<sup>15</sup> Although a *nomen nudum* for lack of description, *melanurus* was subsequently validated as a synonym of *horridus* by Garman, 1883, Mem. Mus. Comp. Zoöl., vol. 8, no. 3, p. 175, and was assigned to the subspecies *atricaudatus* by Klauber, 1936, p. 196.

<sup>16</sup> Although a *nomen nudum* for lack of description, *mexicana* is to be considered a synonym.

## 40 *Classification and Identification*

1940. *Crotalus triseriatus anahuacus* (part) Gloyd, Chi. Acad. Sci. Spec. Pub. no. 4, p. 91.  
1946. *Crotalus gloydi lautus* Smith, Univ. Kans. Sci. Bull., vol. 31, part 1, no. 3, p. 75. Type locality: lava beds 1 km. east of El Limón Totalco, Veracruz, Mexico; type specimen: USNM 110598.  
1952. *Crotalus intermedius intermedius* Klauber, Bull. Zoöl. Soc. San Diego, no. 26, p. 9.

*Range*.—The range of this subspecies is imperfectly known. Specimens have been seen from eastern Hidalgo, northeastern Puebla, and west-central Veracruz (fig. 2:8).

### ***Crotalus intermedius gloydi* Taylor<sup>17</sup>**

#### **Oaxacan Small-Headed Rattlesnake**

Fig. 2:33

1941. *Crotalus triseriatus gloydi* Taylor, Univ. Kans. Sci. Bull., vol. 27, part 1, no. 7, p. 130. Type locality: Cerro San Felipe, elevation 10,000 feet, near [15 km. northeast of] Oaxaca de Juárez, Oaxaca, Mexico; type specimen: EHT-HMS 23645.  
1946. *Crotalus gloydi gloydi* Smith, Univ. Kans. Sci. Bull., vol. 31, part 1, no. 3, p. 78.  
1952. *Crotalus intermedius intermedius* (part) Klauber, Bull. Zoöl. Soc. San Diego, no. 26, p. 9.  
1957. *Crotalus intermedius gloydi* Davis and Dixon, Sw. Nat., vol. 2, no. 1, p. 25.

*Range*.—The range, as presently known, includes mountain areas of central Oaxaca and Michoacán (fig. 2:8).

### ***Crotalus intermedius omiltemanus* Günther**

#### **Omilteman Small-Headed Rattlesnake**

Fig. 2:34

1895. *Crotalus omiltemanus* Günther, Biol. Cent.-Amer., Rept. Batr., p. 192. Type locality: Omilteme, Guerrero, Mexico; type specimens: BM 93.3.15.11 and 95.3.15.11 (newly assigned numbers 1946.1.19.28 and 29).  
1896. *Crotalus triseriatus* (part) Boulenger, Cat. Snakes Brit. Mus., vol. 3, p. 581.  
1936. *Crotalus triseriatus triseriatus* (part) Klauber, Trans. San Diego Soc. Nat. Hist., vol. 8, no. 20, p. 247.  
1938. *Crotalus triseriatus omiltemanus* Klauber, Copeia, no. 4, p. 196.  
1952. *Crotalus intermedius omiltemanus* Klauber, Bull. Zoöl. Soc. San Diego, no. 26, p. 14.

*Range*.—Central Guerrero, Mexico (fig. 2:8).

### ***Crotalus lannomi* Tanner**

#### **Autlán Rattlesnake**

1966. *Crotalus lannomi* Tanner, Herpet., vol. 22, no. 4, p. 298. Type locality: 1.8 mi. west of the pass, Puerto Los Mazos, on Mexican Highway No. 80, Jalisco, Mexico; type specimen: BYU 23800.

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<sup>17</sup> The revival of *C. intermedius gloydi* was suggested by Davis and Dixon (1957, p. 25) based on a newly acquired specimen from Oaxaca. It was their opinion that *i. gloydi* differs from *i. intermedius* of Veracruz and Puebla in having the postnasal in contact with the first supralabial only, and in having the lower preocular in contact with the loreal. I have lately had access to a series of eleven specimens taken by C. M. Bogert in Oaxaca in 1961 and 1963 and find that they usually (27 out of 32 counts in all available specimens) do differ from the Totalcan series in the first character, and therefore I agree with Davis and Dixon in the recognition of *gloydi* as a valid subspecies. I find the second character—the lower preocular-loreal contact—to be variable and, in some cases indeterminate in the new series, as well as in several other specimens, and therefore do not use this character in the segregation of the *intermedius* subspecies.

***Crotalus lepidus lepidus* (Kennicott)****Mottled Rock Rattlesnake****Fig. 2:35**

1861. *Caudisona lepida* Kennicott, Proc. Acad. Nat. Sci. Phila., vol. 13, p. 206. Type localities: Presidio del Norte<sup>18</sup> and Eagle Pass, Texas; type specimens: two heads, now lost.
1866. *Aploaspis lepida* Cope, Proc. Acad. Nat. Sci. Phila., vol. 18, p. 310.
1883. *Crotalus lepidus* (part) Cope, Proc. Acad. Nat. Sci. Phila., vol. 35, p. 13.
1887. *Crotalus (tigris) palmeri* Garman, Bull. Essex Inst., vol. 19, p. 124. Type locality: Monclova, Coahuila, Mexico; type specimen: MCZ 4578.
1936. *Crotalus lepidus lepidus* Gloyd, Occ. Papers Mus. Zool. Univ. Mich., no. 337, p. 2.

*Range*:—Southeastern New Mexico, southwestern Texas, and northeastern Mexico, including: the Carlsbad Caverns area of New Mexico; the trans-Pecos region of Texas (especially the Davis and Chisos mountains, but excluding the El Paso area, where it is replaced by *C. l. klauberi*), together with Val Verde, Real, and Maverick counties; and the Mexican states of eastern Chihuahua, Coahuila, western Nuevo León, western San Luis Potosí, and southeastern Zacatecas (where there is intergradation with *C. l. klauberi*) (fig. 2:7).

***Crotalus lepidus klauberi* Gloyd****Banded Rock Rattlesnake****Figs 2:36 and 2:37**

1883. *Crotalus lepidus* (part) Cope, Proc. Acad. Nat. Sci. Phila., vol. 35, p. 13.
1936. *Crotalus lepidus klauberi* Gloyd, Occ. Papers Mus. Zool. Univ. Mich., no. 337, p. 2. Type locality: Carr Canyon, Huachuca Mountains, Cochise County, Arizona; type specimen: MZUM 79895.
1944. *Crotalus semicornutus* Taylor, Univ. Kans. Sci. Bull., vol. 30, part 1, no. 4, p. 52. Type locality: Mojarachic [near Batopilas], Chihuahua, Mexico; type specimen: EHT-HMS 23014.

*Range*:—Southeastern Arizona, southwestern New Mexico, the El Paso area in Texas, and north-central Mexico, including: the Santa Rita, Huachuca, Dragoon, Dos Cabezas, and Chiricahua mountains of southeastern Arizona; the Franklin, Magdalena, Pinos Altos, Mimbres, Animas, Big Hatchet, and Dog mountains of southwestern New Mexico; El Paso County, Texas; and mountain areas in the Mexican states of northeastern Sonora, southeastern Sinaloa, Chihuahua, Durango, Nayarit,<sup>19</sup> Zacatecas, Aguascalientes, and Jalisco (fig. 2:7).

***Crotalus lepidus morulus* Klauber****Tamaulipan Rock Rattlesnake**

1952. *Crotalus lepidus morulus* Klauber, Bull. Zool. Soc. San Diego, no. 26, p. 52, f.n. Type locality: 10 miles northwest of Gómez Farías on the trail to La Joya de Salas, Tamaulipas, Mexico; type specimen: MZUM 101376.

*Range*:—Mountains northwest of Gómez Farías, and near Chinas, Tamaulipas, Mexico (fig. 2:7).

<sup>18</sup> Smith and Taylor, 1950, Univ. Kans. Sci. Bull., vol. 33, part 2, no. 8, p. 362, subsequently restricted the type locality to Presidio (del Norte), Presidio County, Texas.

<sup>19</sup> The snakes from near the Sinaloa-Durango-Nayarit junction require further study. The five specimens available to me from that relatively inaccessible area key out as *C. l. morulus* or *C. l. lepidus*, although in *C. l. klauberi* territory. An adequate series might justify the recognition of another subspecies.

***Crotalus mitchellii mitchellii*<sup>20</sup> (Cope)**

**San Lucan Speckled Rattlesnake**

**Fig. 2:38**

1861. *Caudisona mitchellii* Cope, Proc. Acad. Nat. Sci. Phila., vol. 13, p. 293. Type locality: Cape St. (= San) Lucas, Baja California, Mexico; type specimen: USNM 5291½, now lost.  
 1875. *Crotalus mitchellii* Cope, in Yarrow, Surv. W. of 100th Merid. (Wheeler), vol. 5, chap. 4, p. 535.  
 1895. *Crotalus mitchellii mitchellii* (part) Stejneger, Rept. U. S. Nat. Mus. for 1893, p. 454.  
 1936. *Crotalus mitchellii mitchellii* Klauber, Trans. San Diego Soc. Nat. Hist., vol. 8, no. 19, p. 154.  
 1952. *Crotalus mitchelli mitchelli* Klauber, Bull. Zool. Soc. San Diego, No. 26, p. 123.

*Range*:—Distrito del Sur of Baja California, Mexico, intergradation with *C. m. pyrrhus* occurring approximately along the border of the southern district with the northern state; also the islands of Cerralvo, Espíritu Santo, San José, Santa Cruz, and Carmen (Gulf coast); and Santa Margarita (Pacific coast) (fig. 2:7).

***Crotalus mitchellii angelensis* Klauber**

**Angel de la Guarda Island Speckled Rattlesnake**

**Fig. 2:39**

1877. *Crotalus pyrrhus*, Streets, Bull. U.S. Nat. Mus., no. 7, p. 39.  
 1887. *Crotalus mitchelli* (part) Belding, West Amer. Sci., vol. 3, no. 24, p. 98.  
 1936. *Crotalus mitchellii pyrrhus* (part) Klauber, Trans. S.D. Soc. Nat. Hist., vol. 8, no. 2, p. 191.  
 1963. *Crotalus mitchelli angelensis* Klauber, Trans. S.D. Soc. Nat. Hist., vol. 13, no. 5, p. 73. Type locality Puerto Refugio, Angel de la Guarda Island, Gulf of California, Mexico; type specimen SDSNH 51994.

*Range*:—Angel de la Guarda Island, Gulf coast of Baja California, Mexico (fig. 2:7).

***Crotalus mitchellii muertensis* Klauber**

**El Muerto Island Speckled Rattlesnake**

**Fig. 2:40**

1949. *Crotalus mitchellii muertensis* Klauber, Trans. San Diego Soc. Nat. Hist., vol. 11, no. 6, p. 97. Type locality: El Muerto Island, Gulf of California, Mexico; type specimen: LMK 37447.  
 1952. *Crotalus mitchelli muertensis* Klauber, Bull. Zool. Soc. San Diego, no. 26, p. 123.

*Range*:—El Muerto Island, San Luis group, Gulf of California coast of Baja California, Mexico (fig. 2:7).

<sup>20</sup> The rule of nomenclature that frowned on the use of a terminal *ii* in names formed from modern personal names and which caused me to eliminate such endings in the first edition of this work is no longer effective. Such *ii* terminations should now be retained, if they were initially so used by the original describer and were proper and valid in other respects. The only rattlesnake names affected are *Crotalus mitchellii* Cope, 1861, and *Sistrurus catenatus edwardsii*, Baird and Girard, 1853. See International Code of Zoological Nomenclature, Second Edition, London, 1964, Art. 32, p. 35; also Art. 31, p. 33 and Appendix D, III, p. 107. [Publisher's Note: Changes in terminations of these two names were made by the author in chapters 2 and 3. They have not been changed elsewhere.]

***Crotalus mitchellii pyrrhus* (Cope)**

**Southwestern Speckled Rattlesnake**

Fig. 2:41

1866. *Caudisona pyrrha* Cope, Proc. Acad. Nat. Sci. Phila., vol. 18, p. 308. Type locality: not stated, but known from the type specimen to be Canyon Prieto, Yavapai County, Arizona; type specimen: USNM 6606.
1875. *Crotalus pyrrhus* Cope, in Yarrow, Surv. W. of 100th Merid. (Wheeler), vol. 5, chap. 5, p. 535.
1895. *Crotalus mitchellii pyrrhus* (part) Stejneger, Rept. U. S. Nat. Mus. for 1893, p. 456.
1922. *Crotalus goldmani* Schmidt, Bull. Amer. Mus. Nat. Hist., vol. 46, art. 11, p. 701. Type locality: El Piñon, elevation, 5,300 ft., San Pedro Mártir Mts., Baja California del Norte, Mexico; type specimen: USNM 37573.
1936. *Crotalus mitchellii pyrrhus* Klauber, Trans. San Diego Soc. Nat. Hist., vol. 8, no. 19, p. 157.
1952. *Crotalus mitchelli pyrrhus* Klauber, Bull. Zool. Soc. San Diego, no. 26, p. 117.

*Range*.—Southern California, southern Nevada, southwestern Utah, western Arizona, northwestern Sonora, and northern Baja California, including the following: California south of the line Barstow-Ivanpah (approximate line of intergradation with *C. m. stephensi*) and east of long. 118°W. (but absent from the San Gabriel Mountains and the Los Angeles coastal plain); the southern tip of Nevada; southwestern corner of Utah, west-central and southwestern Arizona, inside the line Virgin Narrows-Williams-Casa Grande-Ajo; Baja California del Norte, south to the northern boundary of Distrito del Sur (where intergradation with *C. m. mitchellii* is to be expected); extreme northwestern Sonora (fig. 2:7).

***Crotalus mitchellii stephensi* Klauber**

**Panamint Rattlesnake**

Fig. 2:42

1893. *Crotalus tigris* Stejneger, North Amer. Fauna, no. 7, p. 214.
1930. *Crotalus confluentus stephensi* Klauber, Trans. San Diego Soc. Nat. Hist., vol. 6, no. 3, p. 108. Type locality: 2 miles west of Jackass Springs, Panamint Mountains, altitude 6,200 ft., Inyo County, California; type specimen: MVZ 6699.
1936. *Crotalus mitchellii stephensi* Klauber, Trans. San Diego Soc. Nat. Hist., vol. 8, no. 19, p. 162.

*Range*.—The mountain and rocky desert areas of east-central California and southwestern Nevada, including: the eastern slopes of the Sierra Nevada from southern Mono County to southern Kern County, and eastward in California through the desert mountain ranges to the Nevada line; Nevada west and south of the line Hawthorne-Tonopah-St. Thomas. Intergradation with *C. m. pyrrhus* occurs approximately along the line Barstow-Ivanpah-Hoover Dam, which thus constitutes the southern limit of *stephensi* (fig. 2:7).

***Crotalus molossus molossus* Baird and Girard**

**Northern Black-Tailed Rattlesnake**

Fig. 2:43

1853. *Crotalus molossus* Baird and Girard, Cat. North Amer. Rept., part 1, p. 10. Type locality: Fort Webster, Santa Rita del Cobre [Grant County], New Mexico; type specimen: USNM 485.
1854. *Crotalus ornatus* Hallowell, Proc. Acad. Nat. Sci. Phila., vol. 7, p. 192. Type locality: near Pecos River, northwest Texas; type specimen: USNM 486.
1936. *Crotalus molossus molossus* Gloyd, Occ. Papers Mus. Zool. Univ. Mich., no. 325, p. 2.

*Range*.—From central Texas to western Arizona and south in Mexico to southern Coahuila, including: the limestone area north and west of San Antonio, and trans-Pecos Texas; New Mexico southwest of the line Gallup–Albuquerque–Carlsbad; Arizona, from the Grand Canyon and Little Colorado River south, but not including Mohave County; northern Sonora, except the extreme northwest, northern Chihuahua, and northwestern Coahuila. Also Tiburón Island in the Gulf of California. Intergrades with *C. m. nigrescens* in southern Sonora, central Chihuahua, and southern Coahuila<sup>21 22</sup> (fig. 2:2).

***Crotalus molossus estebanensis* Klauber**

**San Esteban Island Rattlesnake**

Fig. 2:44

1922. *Crotalus molossus* (part) Schmidt, Bull. Amer. Mus. Nat. Hist., vol. 46, art. 11, p. 697.  
 1936. *Crotalus molossus molossus* (part) Klauber, Trans. San Diego Soc. Nat. Hist., vol. 8, no. 20, p. 249.  
 1949. *Crotalus molossus estebanensis* Klauber, Trans. San Diego Soc. Nat. Hist., vol. 11, no. 6, p. 104. Type locality: San Esteban Island, Gulf of California, Mexico; type specimen: LMK 26792.

*Range*.—Found only on San Esteban Island, Gulf of California (fig. 2:2).

***Crotalus molossus nigrescens* Gloyd**

**Mexican Black-Tailed Rattlesnake**

Fig. 2:45

1887. *Crotalus molossus* Garman, Bull. Essex Inst., vol. 19, p. 123 (p. 5 of separate).  
 1936. *Crotalus molossus nigrescens* Gloyd, Occ. Papers Mus. Zool., Univ. Mich., no. 325, p. 2. Type locality: 4 miles west of La Colorada, Zacatecas, Mexico; type specimen: MZUM 77833.

*Range*.—The tableland of Mexico from southern Sonora, southwestern Chihuahua, and southern Coahuila (these are the areas of intergradation with *C. m. molossus*), south and east through Durango, Zacatecas, Aguascalientes, western San Luis Potosí, Guanajuato, Querétaro, northwestern Hidalgo, northern Michoacán, México (state), and Distrito Federal, to east-central Veracruz and southeastern Puebla. Probably also occurs in eastern Jalisco, Morelos, Tlaxcala, and northern Oaxaca (fig. 2:2).

***Crotalus polystictus* (Cope)**

**Mexican Lance-Headed Rattlesnake**

1859. *Crotalus lugubris* (part) Jan, Rev. Mag. Zool., ser. 2, vol. 10, pp. 153, 156 (Prod. Icon. Desc. Oph., pp. 30, 31).  
 1863. *Crotalus lugubris* var. *multimaculatus*<sup>23</sup> Jan, Elenco Sist. degli Ofidi, p. 124. Type locality: Mexico; type specimen: Westphal-Castelnau Collection, present disposition unknown. Type locality subsequently restricted to Tupátaro, Guanajuato, by Smith and Taylor, 1950, Univ. Kans. Sci. Bull., vol. 33, part 2, no. 8, p. 330.

<sup>21</sup> The area of intergradation between *molossus* and *nigrescens* is a complicated one, not readily depicted in a brief outline or on a map. For details see Klauber, 1952, p. 91.

<sup>22</sup> I have given further consideration to the relationship between *C. m. molossus* and *C. b. basiliscus* based on additional specimens of the latter from northern Sinaloa and southern Sonora and have not changed my previously expressed opinion that, despite certain tendencies of the northern specimens of *basiliscus* toward *molossus*, they are separate species. It will require material from between Guaymas on the north and Guirocoba and Alamos, Sonora, on the south, to demonstrate whether there are any important evidences of intergradation or hybridization between the two.

<sup>23</sup> The International Commission on Zoölogical Nomenclature, in Opinion 366, Nov. 16, 1955, validated the more generally used name *polystictus* for this snake and suppressed the older name *multimaculatus*.

1865. *Caudisona polysticta* Cope, Proc. Acad. Nat. Sci. Phila., vol. 17, p. 191. Type locality: Table Land, Mexico; type specimen: none designated. Type locality subsequently restricted to Tupátaro, Guanajuato, by Smith and Taylor, 1950, Univ. Kans. Sci. Bull. vol. 33, part 2, no. 8, p. 330.
1875. *Crotalus polystictus* Cope, in Yarrow, Surv. W. of 100th Merid. (Wheeler), vol. 5, chap. 4, p. 533.
1877. *Crotalus jimenezii* Dugès, La Naturaleza, vol. 4, p. 23. Type localities: Silao [Guanajuato], Colima, and Guadalajara; type specimen: none designated. Subsequently the type locality was restricted to Guadalajara, Jalisco, by Smith and Taylor, 1950, Univ. Kans. Sci. Bull., vol. 33, part 2, no. 8, p. 334.

*Range*.—The tableland of central Mexico from southern Zacatecas to central Veracruz, including: southern Zacatecas, Aguascalientes, eastern Jalisco, Guanajuato, Michoacán, Distrito Federal, Morelos, and east-central Veracruz. Probably occurs in the intervening and adjacent states of Querétaro, Hidalgo, México, Tlaxcala, Puebla, and Oaxaca. A record from southeastern Oaxaca needs verification (fig. 2:8).

### *Crotalus pricei pricei* Van Denburgh

#### Western Twin-Spotted Rattlesnake

Figs. 2:46 and 2:47

1895. *Crotalus pricei* Van Denburgh, Proc. Calif. Acad. Sci., ser. 2, vol. 5, p. 856. Type locality: Huachuca Mountains [Cochise County], Arizona; type specimen: Stanford 1702.
1927. *Crotalus triseriatus* Amaral, Bull. Antivenin Inst. Amer., vol. 1, no. 2, p. 52.
1931. *Crotalus triseriatus pricei* Klauber, in Githens and George, Bull. Antivenin Inst. Amer., vol. 5, no. 2, p. 33.
1946. *Crotalus pricei pricei* Smith, Univ. Kans. Sci. Bull., vol. 31, part 1, no. 3, p. 79.

*Range*.—The mountains of southeastern Arizona and northwestern Mexico, including: the Pinaleno (Graham), Santa Rita, Huachuca, and Chiricahua mountains in Arizona; and the Sierra Tarahumare and Sierra Madre in eastern Sonora, western Chihuahua, and Durango (fig. 2:8). Probably occurs in the mountains of eastern Sinaloa and northern Nayarit.

### *Crotalus pricei miquihuanus* Gloyd

#### Eastern Twin-Spotted Rattlesnake

Fig. 2:48

1927. *Crotalus triseriatus* (part) Amaral, Bull. Antivenin Inst. Amer., vol. 1, no. 2, p. 52.
1936. *Crotalus triseriatus triseriatus* (part) Klauber, Trans. San Diego Soc. Nat. Hist., vol. 8, no. 20, p. 248.
1940. *Crotalus triseriatus miquihuanus* Gloyd, Chi. Acad. Sci. spec. pub. no. 4, p. 102. Type locality: Cerro Potosí, near Galeana, Nuevo León, Mexico; type specimen: CNHM 30850.
1946. *Crotalus pricei miquihuanus* Smith, Univ. Kans. Sci. Bull., vol. 31, part 1, no. 3, p. 79.

*Range*.—Southeastern Coahuila, southern Nuevo León, and southwestern Tamaulipas, Mexico (fig. 2:8).<sup>24</sup>

<sup>24</sup> A specimen (MZUM 110878) from near Rincón de Romos, Aguascalientes, Mexico, is temporarily assigned to this subspecies. Its scale characters show it to be more closely related to *C. pricei* than to any other species, and it is slightly nearer to *C. p. miquihuanus* than to *C. p. pricei*. Additional specimens, if like this individual in their major characteristics, will justify the description of a new subspecies, or maybe even of a new species. Unlike the other subspecies of *C. pricei*, this new specimen has undivided dorsal blotches, and they are fewer in number than in the *pricei* subspecies. Superficially the new specimen resembles *pasillus*, from which, however, it differs in important details of squamation.

***Crotalus pusillus* Klauber**

**Tancitaran Dusky Rattlesnake**

Fig. 2:49

1908. *Crotalus triseriatus* Gadow, Through Southern Mexico, p. 513.  
 1936. *Crotalus triseriatus triseriatus* (part) Klauber, Trans. San Diego Soc. Nat. Hist., vol. 8, no. 20, p. 247.  
 1952. *Crotalus pusillus* Klauber, Bull. Zool. Soc. San Diego, no. 26, p. 34. Type locality: Tancitaro, Michoacán, altitude 5,000 feet; type specimen: CNHM 39112.

*Range*.—Mountains of western Michoacán and southern Jalisco, Mexico (fig. 2:10).

***Crotalus ruber ruber* Cope**

**Red Diamond Rattlesnake**

Figs. 2:50 and 2:51

1883. *Crotalus adamanteus atrox* (part) Yarrow, Bull. U. S. Nat. Mus., no. 24, p. 75.  
 1892. *Crotalus adamanteus ruber* Cope, Proc. U. S. Nat. Mus., vol. 14, p. 690. Type locality: undesignated; type specimen: USNM 9209, recorded as being from southern California. Type locality subsequently restricted to Dulzura, San Diego County, California, by Smith and Taylor, 1950, Univ. Kans. Sci. Bull., vol. 33, part 2, no. 8, p. 356.  
 1895. *Crotalus ruber* Van Denburgh, Proc. Calif. Acad. Sci., ser. 2, vol. 5, p. 1007.  
 1895. *Crotalus atrox ruber* Stejneger, Rept. U. S. Nat. Mus. for 1893, p. 439.  
 1917. *Crotalus exsul* (part) Grinnell and Camp, Univ. Calif. Publ. Zool., vol. 17, no. 10, p. 196.  
 1922. *Crotalus atrox elegans* Schmidt, Bull. Amer. Mus. Nat. Hist., vol. 46, art. 11, p. 699. Type locality: Ángel de la Guarda Island, Gulf of California, Mexico; type specimen: USNM 64452.  
 1949. *Crotalus ruber ruber* Klauber, Trans. San Diego Soc. Nat. Hist., vol. 11, no. 5, p. 59.

*Range*.—The Californias from lat. 34° to lat. 26°N., including: southeastern Los Angeles and Orange counties (but excluding the Los Angeles–Santa Ana plain), the southwesterly Morongo area of San Bernardino County, Riverside County west of the desert, San Diego County, and extreme southwestern Imperial County; Baja California, Mexico (but excluding the deserts of the north lying east of the Sierra Juárez), south to Loreto, where there is intergradation with *C. r. lucasensis*. Also Monserrate, San Marcos, South San Lorenzo, Pond, and Ángel de la Guarda islands, all in the Gulf of California (fig. 2:1).

***Crotalus ruber lucasensis* Van Denburgh**

**San Lucan Diamond Rattlesnake**

Fig. 2:52

1861. *Caudisona atrox sonoraensis* (part) Cope, Proc. Acad. Nat. Sci. Phila., vol. 13, p. 292.  
 1875. *Crotalus adamanteus atrox* (part) Cope, Bull. U. S. Nat. Mus., no. 1, p. 33.  
 1920. *Crotalus lucasensis* Van Denburgh, Proc. Calif. Acad. Sci., ser. 4, vol. 10, no. 2, p. 29. Type locality: Agua Caliente, Cape region of Baja California; type specimen: CAS 45888.  
 1922. *Crotalus atrox lucasensis* Schmidt, Bull. Amer. Mus. Nat. Hist., vol. 46, art. 11, p. 698.  
 1949. *Crotalus ruber lucasensis* Klauber, Trans. San Diego Soc. Nat. Hist., vol. 11, no. 5, p. 59.

*Range*.—The southern part of the Baja California peninsula from Loreto (where there is intergradation with *C. r. ruber*) south to Cape San Lucas. Also Santa Margarita and San José islands (fig. 2:1).

***Crotalus scutulatus scutulatus* (Kennicott)**

**Mojave Rattlesnake**

**Figs. 2:53 and 2:54**

1861. *Caudisona scutulata* Kennicott, Proc. Acad. Nat. Sci. Phila., vol. 13, p. 207. Type locality: not given; type specimen: none designated.<sup>25</sup> Type locality subsequently restricted to Wickenburg, Maricopa County, Arizona, by Smith and Taylor, 1950, Univ. Kans. Sci. Bull., vol. 33, part 2, no. 8, p. 353.
1875. *Crotalus scutulatus* Cope in Yarrow, Surv. W. of 100th Merid. (Wheeler), vol. 5, chap. 4, p. 533; see also p. 992.
1875. *Crotalus adamanteus scutulatus* Cope, Bull. U. S. Nat. Mus., no. 1, p. 33.
1895. *Crotalus atrox* (part) Stejneger, Rept. U. S. Nat. Mus. for 1893, p. 436.
1929. *Crotalus confluentus kellyi* Amaral, Bull. Antivenin Inst. Amer., vol. 2, no. 4, p. 91. Type locality: Needles, California; type specimen: LMK 194.
1940. *Crotalus scutulatus scutulatus* Gloyd, Chi. Acad. Sci., spec. pub. 4, p. 200.

*Range*:—From the Mojave Desert in California southeast to south-central Mexico, including: Kern, Los Angeles (Antelope Valley), and San Bernardino counties in California, but only on the desert side of the Tehachapi, San Gabriel, and San Bernardino mountains; the desert valleys of Lincoln and Clark counties, Nevada; extreme southwestern Utah; Arizona south and west of the line Pierce Ferry–Sedona–Safford; extreme southwestern New Mexico; trans-Pecos Texas; northern Sonora, Chihuahua, Durango, western and southern Coahuila, southern Nuevo León, southwestern Tamaulipas, Zacatecas, Aguascalientes, and San Luis Potosí. Probably occurs in eastern Jalisco, northern Guanajuato, and northwestern Querétaro (fig. 2:9).

***Crotalus scutulatus salvini* Günther**

**Huamantlan Rattlesnake**

1895. *Crotalus salvini* Günther, Biol. Cent.-Amer., Rept. Batr., p. 193. Type locality: Huamantla [Tlaxcala], Mexico, altitude 8,000 feet; type specimen: BM 73.1.13.1 (later changed to 1946.1.19.35).
1896. *Crotalus scutulatus* (part) Boulenger, Cat. Snakes Brit. Mus., vol. 3, p. 575.
1940. *Crotalus scutulatus salvini* Gloyd, Chi. Acad. Sci., spec. pub. 4, p. 201.

*Range*:—Querétaro, Tlaxcala, Puebla, and west-central Veracruz. Probably occurs in Hidalgo (fig. 2:9).

***Crotalus stejnegeri* Dunn**

**Long-Tailed Rattlesnake**

**Fig. 2:55**

1919. *Crotalus stejnegeri* Dunn, Proc. Biol. Soc. Wash., vol. 32, p. 214. Type locality: Plumosas (= Plomosas), Sinaloa, Mexico; type specimen: USNM 46586.

*Range*:—The mountains of southeastern Sinaloa and western Durango, Mexico, (fig. 2:10).

<sup>25</sup> Cope (1900, p. 1160) refers to USNM 5021 as the type of *C. scutulatus*, but there is nothing in the museum catalogue to confirm this. USNM 5021 is actually the head of a *C. v. cerberus* or *C. v. helleri*. USNM 5027 is a *scutulatus*, and may have been the specimen Cope had in mind. Both specimens were sent in by Dr. B. J. D. Irwin, and, although ostensibly from Fort Buchanan, Arizona, may have come from California or elsewhere, as indicated by other specimens in the same shipment. USNM 5027 was originally catalogued as "*Caudisona lepturus*" under date of January 30, 1861. This may be a name originally contemplated by Kennicott for this species, which would suggest that this was the type, although Kennicott's counts of the labials are not the same as those of No. 5027.

***Crotalus tigris* Kennicott**

**Tiger Rattlesnake**

Fig. 2:56

1859. *Crotalus tigris* Kennicott, in Baird, Repts. of Boundary, U. S. Mex. Boundary, Surv., vol. 2, p. 14. Type locality: Sierra Verde and Pozo Verde (modern maps show the Sierra Pozo Verde on the Sonoran side of the U. S.-Mexican boundary near Sasabe, Sonora); type specimen: USNM 471. USNM 472-3 may be considered cotypes. No. 473 is now PANS 7160.
1931. *Crotalus tigris* Klauber, Trans. San Diego Soc. Nat. Hist., vol. 6, no. 24, p. 356.

*Range*:—The rocky desert foothills of south-central Arizona, and Sonora, from north of Phoenix, Arizona, via Tucson, to southern Sonora, Mexico, including the following Arizona mountain ranges: Humbug, Phoenix, Salt River, Estrella, Santa Catalina, Tucson, Coyote, Baboquivari (Verde), Sierrita, and Santa Rita (fig. 2:7).

***Crotalus tortugensis* Van Denburgh and Slevin**

**Tortuga Island Diamond Rattlesnake**

Fig. 2:57

1921. *Crotalus tortugensis* Van Denburgh and Slevin, Proc. Calif. Acad. Sci., ser. 4, vol. 11, no. 17, p. 398. Type locality: Tortuga Island, Gulf of California, Mexico; type specimen: CAS 50515.
1929. *Crotalus atrox sonoraensis* (part) Amaral, Bull. Antivenin Inst. Amer., vol. 2, no. 4, p. 85.
1933. *Crotalus atrox tortugensis* Stejneger and Barbour, Check List, N. Amer. Amp. Rept., ed. 3, p. 133.

*Range*:—Known only from the type locality (fig. 2:1).

***Crotalus transversus* Taylor**

**Cross-Banded Mountain Rattlesnake**

1940. *Crotalus triseriatus anahuacus* Martin del Campo, Anales Inst. Biol. Mex., vol. 11, no. 2, p. 742.
1944. *Crotalus transversus* Taylor, Univ. Kans. Sci. Bull., vol. 30, part 1, no. 4, p. 47. Type locality: near Tres Marias (Tres Cumbres), about 55 km. southwest of Mexico, D. F. in Morelos<sup>26</sup> Mexico, elevation about 10,000 ft.; type specimen: EHT-HMS 30001.

*Range*:—México (state), Distrito Federal, and northwestern Morelos (fig. 2:8).

***Crotalus triseriatus triseriatus* (Wagler)**

**Central-Plateau Dusky Rattlesnake**

Fig. 2:58

1830. *Uropsophus triseriatus* Wagler, Nat. Syst. Amph., p. 176. Type locality: Mexico; type specimen: originally in the collection of the König. Univers. zu Berlin. Type locality subsequently restricted to Alvarez, San Luis Potosí, by Smith and Taylor, 1950, Univ. Kans. Sci. Bull., vol. 33, part 2, no. 8, p. 342.<sup>27</sup>
1831. *Crotalus triseriatus* Gray, Synopsis Spec. Class Rept. in Griffith's Animal Kingdom by Cuvier, vol. 9, p. 78.
1859. *Crotalus lugubris* Jan, Rev. Mag. Zoöl., ser. 2, vol. 10, pp. 153, 156 (Prod. Icon. Desc. Ophid., pp. 28, 31). Type locality: Mexico; type specimen: Milan 1414,<sup>28</sup> now destroyed.

<sup>26</sup> Davis and Smith (Herpetologica, vol. 8, part 4, p. 141) give reasons for considering Laguna Zempoala, state of México, to be the type locality.

<sup>27</sup> This restriction is not valid, since *triseriatus triseriatus*, as now defined, does not range into San Luis Potosí. Alvarez is the type locality of the subspecies *C. t. aquilus*.

<sup>28</sup> This species was originally composite. The lectotype was fixed by Klauber, Copeia, no. 1, p. 17, 1940.

1895. *Crotalus pallidus* Günther, Biol. Cent.-Amer., Rept. Batr., p. 193. Type locality: City of Mexico; type specimen: BM 68.4.7.23 (newly assigned number 1946.1.17.70).
1931. *Crotalus triseriatus triseriatus* (part) Klauber, in Githens and George, Bull. Antivenin Inst. Amer., vol. 5, no. 2, p. 33.
1940. *Crotalus triseriatus triseriatus* (part) Gloyd, Chi. Acad. Sci. spec. pub. 4, p. 84.
1940. *Crotalus triseriatus anahuacus* Gloyd, Chi. Acad. Sci. spec. pub. 4, p. 91. Type locality: Valley of Mexico; type specimen: MCZ 33681. Type locality subsequently restricted to Coyoacán, Distrito Federal, Mexico, by Smith and Taylor, 1950, Univ. Kans. Sci. Bull., vol. 33, part 2, no. 8, p. 329.
1952. *Crotalus triseriatus triseriatus* Klauber, Bull. Zoöl. Soc. San Diego, no. 26, p. 19.

*Range*.—Central Mexico from Nayarit to west-central Veracruz, including: Nayarit, Jalisco, Michoacán, México (state), Distrito Federal, Morelos, Puebla, and west-central Veracruz. Probably occurs in Tlaxcala (fig. 2:7).

### *Crotalus triseriatus aquilus* Klauber

#### Queretaran Dusky Rattlesnake

Fig. 2:59

1877. *Crotalus lugubris* Dugès, La Naturelleza, vol. 4, p. 25.
1885. *Crotalus triseriatus* Cope, Proc. Amer. Philos. Soc., vol. 22, p. 286.
1931. *Crotalus triseriatus triseriatus* (part) Klauber, in Githens and George, Bull. Antivenin Inst. Amer., vol. 5, no. 2, p. 33.
1952. *Crotalus triseriatus aquilus* Klauber, Bull. Zoöl. Soc. San Diego, no. 26, p. 24. Type locality: near Alvarez, San Luis Potosí, Mexico; type specimen: MCZ 27843.

*Range*.—Southern San Luis Potosí, Guanajuato, northeastern Michoacán, Querétaro, northern México (state), and Hidalgo, Mexico. Will probably be found in northwestern Veracruz (fig. 2:7).

### *Crotalus unicolor* van Lidth de Jeude

#### Aruba Island Rattlesnake

Fig. 2:60

1887. *Crotalus horridus* var. *unicolor* van Lidth de Jeude, Notes Leyden Mus., vol. 9, no. 8, p. 133. Type locality: Aruba Island, Netherlands West Indies; type specimens: Leyden Mus. 613 and 1579 (see Brongersma below).
1896. *Crotalus terrificus* (part) Boulenger, Cat. Snakes Brit. Mus., vol. 3, p. 573 (574).
1905. *Crotalus pulvis* Ditmars, Ninth Ann. Rept. N.Y. Zoöl. Soc., p. 199. Type locality: Managua, Nicaragua [actual locality doubtful]; type specimen: MCZ 7044.
1936. *Crotalus unicolor* Klauber, Occ. Papers San Diego Soc. Nat. Hist., no. 1, p. 4.
1937. *Crotalus terrificus terrificus* (part) Amaral, Mem. Inst. Butantan, vol. 10, no. 8, p. 161 (162).
1940. *Crotalus durissus unicolor* Brongersma, Studies of Fauna of Curaçao, Aruba, Bonaire and the Venezuelan Islands, no. 8, p. 131 (p. 18 of separate).

*Range*.—Aruba Island, off the coast of Venezuela (fig. 2:5).

### *Crotalus vegrandis* Klauber

#### Uracoan Rattlesnake

Fig. 2:61

1941. *Crotalus vegrandis* Klauber, Trans. San Diego Soc. Nat. Hist., vol. 9, no. 30, p. 334. Type locality: Maturín Savannah, near Uracoa, Sotillo District, state of Monagas, Venezuela; type specimen: CM 17384.

*Range*.—Known only from the type locality (fig. 2:5).

***Crotalus viridis viridis* (Rafinesque)****Prairie Rattlesnake**

Fig. 2:62

1818. *Crotalinus viridis* Rafinesque, Amer. Month. Mag. & Crit. Rev., vol. 4, no. 1, p. 41. Type locality: the Upper Missouri [Valley]; type specimen: none designated. Type locality subsequently restricted to Gross, Boyd County, Nebraska, by Smith and Taylor, 1950, Univ. Kans. Sci. Bull., vol. 33, part 2, no. 8, p. 358.
1820. *Crotalurus viridis* Rafinesque, Ann. Nat., no. 1, p. 5.
1823. *Crotalus confluentus* Say, in Long's Exped. from Pittsburgh to Rocky Mountains, edited by Edwin James, vol. 2, p. 48, footnote. Type locality: vicinity of the Rocky Mountains;<sup>20</sup> type specimen: in Philadelphia Museum, present disposition unknown.
1852. *Crotalus lecontei* Hallowell, Proc. Acad. Nat. Sci. Phila., vol. 6, p. 180. Type locality: Cross Timbers [in what is now Oklahoma]; type specimen: USNM 4233, now lost.<sup>20</sup>
1883. *Crotalus confluentus* var. *pulverulentus* Cope, Proc. Acad. Nat. Sci. Phila., vol. 35, p. 11. Type locality: Lake Valley [Sierra County], New Mexico; type specimen: PANS 10745.
1883. *Crotalus confluentus* var. *confluentus* Cope, Proc. Acad. Nat. Sci. Phila., vol. 35, p. 11.
1936. *Crotalus viridis viridis* Klauber, Trans. San Diego Soc. Nat. Hist., vol. 8, no. 2, p. 191.

*Range*:—The Great Plains from long. 96° W. to the Rocky Mountains and from southern Canada to extreme northern Mexico, including the following: southwestern Saskatchewan (south of the South Saskatchewan River and west of long. 107° 30' W.); southeastern Alberta (south of the Red Deer River and east of long. 113° W.); Montana, except the higher mountains in the west; the Lemhi Valley in Idaho; Wyoming east of the Rockies; Colorado (except in the higher mountains, and in the basins of the Colorado and Green rivers west of the Continental Divide); extreme southeastern Utah and northeastern Arizona (San Juan River basin); New Mexico, except the west-central mountains; extreme northeastern Sonora, northern Chihuahua, and northern Coahuila, near the U. S. boundary; southwestern North Dakota (west of the Missouri River but including the first tier of counties on the eastern bank); western, central, and extreme southeastern South Dakota; Plymouth and Woodbury counties, western Iowa; central and western Nebraska; central and western Kansas; Oklahoma west of Woods and Custer counties; the Panhandle, and western and southwestern Texas. This rattler of the western Mississippi basin plains intergrades with *C. v. oreganus* in east-central Idaho; with *C. v. nuntius* in northeastern Arizona; and with *C. v. concolor* in southeastern Utah (fig. 2:6).

***Crotalus viridis abyssus* Klauber****Grand Canyon Rattlesnake**

Fig. 2:63

1930. *Crotalus confluentus abyssus* Klauber, Trans. San Diego Soc. Nat. Hist., vol. 6, no. 3, p. 114. Type locality: Tanner Trail, 300 ft. below the south rim of the Grand Canyon, Coconino County, Arizona; type specimen: LMK 2216.
1936. *Crotalus viridis abyssus* Klauber, Trans. San Diego Soc. Nat. Hist., vol. 8, no. 20, p. 191.

*Range*:—The Grand Canyon of the Colorado River, Grand Canyon National Park, Arizona, from the north to the south rim. Intergrades with *C. v. nuntius* along the south rim, and with *C. v. lutosus* in the northwest corner of its range (fig. 2:6).

<sup>20</sup> From the itinerary on the date (July 18, 1820) when the type was said to have been collected, the type locality can be presumed to be the vicinity of Bell Springs, Colorado.

<sup>20</sup> See Stejneger in Amaral, Bull. Antivenin Inst. Amer., vol. 2, no 4, p. 87.

***Crotalus viridis caliginis* Klauber**

**Coronado Island Rattlesnake**

Fig. 2:64

1877. *Crotalus adamanteus atrox* Streets, Bull. U. S. Nat. Mus., no. 7, p. 40.  
 1896. *Crotalus confluentus* (part) Boulenger, Cat. Snakes Brit. Mus., vol. 3, p. 576.  
 1905. *Crotalus oregonus* Van Denburgh, Proc. Calif. Acad. Sci., ser. 3, vol. 4, no. 1, p. 18.  
 1929. *Crotalus confluentus oregonus* (part) Amaral, Bull. Antivenin Inst. Amer., vol. 2, no. 4, p. 92.  
 1936. *Crotalus viridis oregonus* (part) Klauber, Trans. San Diego Soc. Nat. Hist., vol. 8, no. 20, p. 191.  
 1949. *Crotalus viridis caliginis* Klauber, Trans. San Diego Soc. Nat. Hist., vol. 11, no. 6, p. 90.  
 Type locality: South Coronado Island, northwest coast of Baja California, Mexico; type specimen: LMK 2800.

*Range*:—Known only from the type locality (fig. 2:6).

***Crotalus viridis cerberus* (Coues)**

**Arizona Black Rattlesnake**

Fig. 2:65

1866. *Caudisoma lucifer* Cope, Proc. Acad. Nat. Sci. Phila., vol. 18, p. 307.  
 1875. *Caudisoma lucifer* var. *cerberus* Coues, Surv. W. of 100th Merid. (Wheeler), vol. 5, chap. 5, p. 606. Type locality: San Francisco Mountains, Coconino County, Arizona; type specimens: field numbers 509 (= PANS 7085?) and 511 (= PANS 7088). There were two other syntypes, PANS 7086-7, whose present whereabouts is not known.  
 1883. *Crotalus oregonus* var. *cerberus* Garman, Mem. Mus. Comp. Zool., vol. 8, no. 3, p. 137.  
 1936. *Crotalus viridis oregonus* (part) Klauber, Trans. San Diego Soc. Nat. Hist., vol. 8, no. 20, p. 191.  
 1949. *Crotalus viridis cerberus* Klauber, Trans. San Diego Soc. Nat. Hist., vol. 11, no. 6, p. 83.

*Range*:—Arizona, from the Hualpai Mountains and Cottonwood Cliffs in the northwest, southeast to the Santa Catalina, Rincon, Pinaleno, and Blue mountains; also Steeple Rock, in extreme western New Mexico (fig. 2:6).

***Crotalus viridis concolor* Klauber**

**Midget Faded Rattlesnake**

Fig. 2:66

1915. *Crotalus oregonus* (part) Van Denburgh and Slevin, Proc. Calif. Acad. Sci., ser. 4, vol. 5, no. 4, p. 109.  
 1929. *Crotalus concolor*<sup>21</sup> Woodbury, Bull. Univ. of Utah, vol. 20, no. 6, p. [2]. Type locality: King's Ranch, at the base of the Henry Mountains, Garfield County, Utah; type specimen: Utah 306.  
 1930. *Crotalus confluentus decolor* Klauber, Trans. San Diego Soc. Nat. Hist., vol. 6, no. 3, p. 111. Type locality: Grand Junction, Mesa County, Colorado; type specimen: CNHM 923.  
 1936. *Crotalus viridis concolor* Klauber, Trans. San Diego Soc. Nat. Hist., vol. 8, no. 20, p. 191.  
 1940. *Crotalus viridis decolor* Gloyd, Chi. Acad. Sci. spec. pub. 4, p. 216.

*Range*:—The basins of the Colorado and Green rivers, including: a small area in southwestern Wyoming; Utah east of long. 111° W., except the southeastern corner; and extreme east-central Colorado (fig. 2:6).

<sup>21</sup> The International Commission on Zoölogical Nomenclature in Opinion 339, March 17, 1955, validated *concolor* as the name for this snake, suppressing *concolor* Jan. 1859, a synonym of *horridus*. *C. v. concolor* Woodbury, 1929, takes precedence over *C. v. decolor* Klauber, 1930..

***Crotalus viridis helleri* Meek****Southern Pacific Rattlesnake****Fig. 2:67**

1859. *Crotalus lecontei* (part) Hallowell (not of Hallowell, 1852), Pac. R. R. Surv. (Williamson route), vol. 10, part 4, p. 18.
1859. *Crotalus lucifer* Cope, Proc. Acad. Nat. Sci. Phila., vol. 11, p. 337.
1883. *Crotalus confluentus* var. *lucifer* (part) Cope, Proc. Acad. Nat. Sci. Phila., vol. 35, p. 11.
1898. *Crotalus oregonus* (part) Van Denburgh, Proc. Amer. Philos. Soc., vol. 37, no. 157, p. 141.
1905. *Crotalus helleri* Meek, Field Col. Mus., Zoöl. Ser., vol. 7, no. 1, pub. 104, p. 7. Type locality: San José [lat. 31° N.], Baja California, Mexico; type specimen: CNHM 1272.
1929. *Crotalus confluentus oregonus* (part) Amaral, Bull. Antivenin Inst. Amer., vol. 2, no. 4, p. 92.
1936. *Crotalus viridis oregonus* (part) Klauber, Trans. San Diego Soc. Nat. Hist., vol. 8, no. 20, p. 191.
1949. *Crotalus viridis helleri* Klauber, Trans. San Diego Soc. Nat. Hist., vol. 11, no. 6, p. 77.

*Range*:—Southern California and northern Baja California, west of the desert, from southwestern San Luis Obispo and Kern counties, through Santa Barbara, Ventura, Los Angeles, southwestern San Bernardino, Orange, western Riverside, San Diego, and extreme southwestern Imperial counties; also south through Baja California to lat. 28° 30' N.; also Santa Catalina Island, Los Angeles County, California. Intergrades with *C. v. oregonus* along the line Lebec-Shandon-Cape San Martin (fig. 2:6).

***Crotalus viridis lutosus* Klauber****Great Basin Rattlesnake****Fig. 2:68**

1859. *Crotalus lucifer* Baird, Pac. R. R. Surv. (Williamson), vol. 10, part 4, p. 10.
1875. *Crotalus confluentus* (part) Yarrow, Surv. W. of 100th. Merid. (Wheeler), vol. 5, chap. 1, p. 530.
1883. *Crotalus confluentus lucifer* (part) Cope, Proc. Acad. Nat. Sci. Phila., vol. 35, pp. 11, 19, 22.
1892. *Crotalus confluentus lecontei* Cope, Proc. U. S. Nat. Mus., vol. 14, no. 882, p. 692.
1898. *Crotalus oregonus* (part) Van Denburgh, Proc. Amer. Philos. Soc., vol. 37, no. 157, p. 141.
1929. *Crotalus confluentus kellyi* (part) Amaral, Bull. Antivenin Inst. Amer., vol. 2, no. 4, p. 91.<sup>32</sup>
1930. *Crotalus confluentus lutosus* Klauber, Trans. San Diego Soc. Nat. Hist., vol. 6, no. 3, p. 100. Type locality: 10 miles northwest of Abraham on the road to Joy, Millard County, Utah; type specimen: LMK 1814.
1936. *Crotalus viridis lutosus* Klauber, Trans. San Diego Soc. Nat. Hist., vol. 8, no. 20, p. 191.

*Range*:—The Great Basin between the Rocky Mountains and the Sierra Nevada including: Idaho south of lat. 44° N.; Utah west of long. 111° W.; Arizona north and west of the Colorado River and the north rim of the Grand Canyon; all Nevada except Esmeralda, southern Nye, and Clark counties; California, east of the Sierra Nevada, from Lower Klamath Lake south to below Mono Lake; Oregon south and east of the line Upper Klamath Lake-Fort Rock-Burns-Council (Idaho), this being the approximate line of intergradation with *C. v. oregonus* (fig. 2:6).

***Crotalus viridis nuntius* Klauber****Hopi Rattlesnake****Fig. 2:69**

1883. *Crotalus confluentus* (part) Yarrow, Bull. U. S. Nat. Mus., no. 24, p. 77.<sup>33</sup>
1935. *Crotalus confluentus nuntius* Klauber, Trans. San Diego Soc. Nat. Hist., vol. 8, no. 13.

<sup>32</sup> Amaral's *kellyi* was a composite of *C. v. lutosus* and *C. s. scutulatus*. Because the types belonged to the latter subspecies, *kellyi* must be considered a synonym of *scutulatus*.

<sup>33</sup> This reference is based on USNM 4251, a specimen of *nuntius* from San Francisco Mountain, Arizona, although incorrectly stated by Yarrow to have come from San Francisco, California.

- p. 78. Type locality: Canyon Diablo, Coconino County, Arizona; type specimen: LMK 3105.  
1936. *Crotalus viridis nuntius* Klauber, Trans. San Diego Soc. Nat. Hist., vol. 8, no. 20, p. 191.

*Range*.—Northeastern and north-central Arizona from the New Mexican line to Cateract Creek, including the following: the basin of the Little Colorado River; the southern part of the Apache Indian Reservation; the Hopi Indian Reservation; and the Coconino Plateau, from the south rim of the Grand Canyon south to U. S. Highway 66. Intergrades with *C. v. viridis* along the northeastern edge of its range, and with *C. v. abyssus* along the south rim of the Grand Canyon (fig. 2:6).

### *Crotalus viridis oreganus* Holbrook

#### Northern Pacific Rattlesnake

Figs. 2:70 and 2:71

1840. *Crotalus oreganus* Holbrook, North Amer. Herp., ed. 1, vol. 4, p. 115. Type locality: banks of the Oregon or Columbia River [probably between Walla Walla, Washington, and the Pacific Coast]; type specimen: PANS 7158. Type locality subsequently restricted to The Dalles, Wasco County, Oregon, by Smith and Taylor, 1950, Univ. Kans. Sci. Bull., vol. 33, part 2, no. 8, p. 360.  
1852. *Crotalus lucifer* Baird and Girard, Proc. Acad. Nat. Sci. Phila., vol. 6, p. 177. Type locality: Oregon and California; type specimen: USNM 7762 (Oregon).  
1859. *Crotalus lecontei* Hallowell, Pac. R. R. Surv. (Williamson), vol. 10, part 4, no. 1, p. 18.  
1868. *Crotalus hallowelli* Cooper, in Cronise, Nat. Wealth Calif., p. 483. Type locality: southern counties [of California] west of the Sierra; type specimen: none designated. A *nomen nudum* for lack of description.<sup>14</sup>  
1883. *Crotalus confluentus lucifer* Cope, Proc. Acad. Nat. Sci. Phila., vol. 35, p. 11.  
1929. *Crotalus confluentus oreganus* (part) Amaral, Bull. Antivenin Inst. Amer., vol. 2, no. 4, p. 92.  
1936. *Crotalus viridis oreganus* (part) Klauber, Trans. San Diego Soc. Nat. Hist., vol. 8, no. 20, p. 191.  
1949. *Crotalus viridis oreganus* Klauber, Trans. San Diego Soc. Nat. Hist., vol. 11, no. 6, p. 67.

*Range*.—The Pacific slope from British Columbia south to San Luis Obispo and Kern counties in California, including the following: south-central British Columbia within the triangle Lillooet-Shushwap Lake-Osoyoos, and east along the U. S. border to Christina Lake, and possibly to Waneta; Washington, east of the Cascade Mountains (except the extreme northeastern corner; the western edge of Idaho from Coeur d'Alene south to near Council and Weiser; northern and western Oregon, but not in the Cascade Mountains; and California west of the Sierra Nevada, south to San Luis Obispo and Kern counties. Also Morro Rock off San Luis Obispo County. Intergrades with *C. v. viridis* up to the Clearwater and Salmon Rivers in Idaho; with *lutosus* in western Idaho, southeastern Oregon, and northeastern California; and with *C. v. helleri* at about the line Lebec-Shandon-Cape San Martin in Kern and San Luis Obispo counties (fig. 2:6).

Amaral, Bull. Antivenin Inst. Amer., vol. 2, no. 4, p. 91, 1929, considered specimens of this form to be intermediate between *Crotalus confluentus confluentus* (= *C. v. viridis*) and *C. c. kellyi*. His *C. c. kellyi* was a composite of *C. v. lutosus* and *C. s. scutulatus*; the type specimens belong to the latter subspecies.

<sup>14</sup> Subsequently placed in the synonymy of *C. v. oreganus* (with a question mark) by Stejneger, 1895, Rept. U. S. Nat. Mus. for 1893, p. 445, and (without question mark) by Van Denburgh, 1922, Occ. Papers Calif. Acad. Sci., no. 10, vol. 2, p. 932.

***Crotalus willardi willardi* Meek**

**Arizona Ridge-Nosed Rattlesnake**

Fig. 2:72

1905. *Crotalus willardi* Meek, Field Columbian Mus., pub. 104., Zoöl. Ser., vol. 7, no. 1, p. 18.  
Type locality: above Hamburg, middle branch of Ramsey Canyon, Huachuca Mountains (altitude about 7,000 ft.), Cochise County, Arizona;<sup>35</sup> type specimen: CNHM 902.  
1949. *Crotalus willardi willardi* Klauber, Trans. San Diego Soc. Nat. Hist., vol. 11, no. 8, p. 125.

*Range*.—The Huachuca and Santa Rita mountains of southeastern Arizona; and the Sierra de los Ajos and Sierra Azul in northern Sonora (fig. 2:3).

***Crotalus willardi amabilis* Anderson**

**Del Nido Ridge-Nosed Rattlesnake**

Fig. 2:73

1962. *Crotalus willardi amabilis* Anderson, Copeia, no. 1, p. 160. Type locality: Arroyo Mesteño, Sierra del Nido, Chihuahua, Mexico, altitude 8,500 ft.; type specimen: MVZ 68896.

*Range*.—Known only from the Sierra del Nido, north-central Chihuahua, Mexico (fig. 2:3).

***Crotalus willardi meridionalis* Klauber**

**Southern Ridge-Nosed Rattlesnake**

Fig. 2:74

1936. *Crotalus willardi* (part) Klauber, Trans. San Diego Soc. Nat. Hist., vol. 8, no. 20, p. 231.  
1949. *Crotalus willardi meridionalis* Klauber, Trans. San Diego Soc. Nat. Hist., vol. 11, no. 8, p. 131. Type locality: Coyotes, Durango, Mexico, altitude 8,000 ft.; type specimen: LMK 6569.

*Range*.—Southern Durango and southwestern Zacatecas, in west-central Mexico (fig. 2:3).

***Crotalus willardi silus* Klauber**

**West Chihuahua Ridge-Nosed Rattlesnake**

Fig. 2:75

1917. *Crotalus willardi* (part) Stejneger and Barbour, Check List of North Amer. Amph. and Rept. [ed. 1], p. 111.  
1949. *Crotalus willardi silus* Klauber, Trans. San Diego Soc. Nat. Hist., vol. 11, no. 8, p. 128. Type locality: on the Río Gavilán, 7 mi. southwest of Pacheco, Chihuahua, Mexico, altitude 6,200 ft.; type specimen: MVZ 46694.

*Range*.—Northeastern Sonora and western Chihuahua, Mexico, and southwestern New Mexico (fig. 2:3).

**Genus *Sistrurus* Garman**

1766. *Crotalus* (part) Linné, Syst. Nat., ed. 12, p. 372.  
1820. *Crotulurus* (misprint for *Crotalurus*), Rafinesque, Ann. Nat. no. 1, p. 5. Type *catenatus* Syn. *Crotalus* Linné, 1758.  
1822. *Crotalus* Fleming, Philos. of Zoöl., vol. 2, p. 294. Type *miliaris* [sic]. Not of Linné, 1758.

<sup>35</sup> Meek originally reported the type locality as Tombstone, Cochise County; but Swarth, 1921, Copeia, no. 100, p. 83, on the basis of data secured from Frank C. Willard, the original collector, made the correction here accepted.

1825. *Crotalophorus* Gray, Annals of Philos., n.s., vol. 10, art. 8, p. 205. Type *miliaris* [sic]. Not of Houttuyn, 1764.  
 1826. *Caudisona* Fitzinger, Neue Class. Rept., pp. 34, 63. Type *miliaria*. Not of Laurenti, 1768.  
 1883. *Sistrurus*<sup>m</sup> Garman, Mem. Mus. Comp. Zoöl., vol. 8, no. 3, pp. xxvii, 110, 118, 176. Type *miliaris* by generic substitution (Rules Zoöl. Nomen., art. 30, 1926, ii, f.).

***Sistrurus catenatus catenatus* (Rafinesque)**

Eastern Massasauga

Fig. 2:76

1818. *Crotalinus catenatus* Rafinesque, Amer. Month. Mag. & Crit. Rev., vol. 4, no. 1, p. 41. Type locality: prairies of the Upper Missouri; type specimen: none designated. Type locality restricted to Kansas City, Mo., by Schmidt, 1953, p. 226.  
 1820. *Crotulurus catenatus* Rafinesque, Ann. Nat. no. 1, p. 5.  
 1838. *Crotalus messasaugus* Kirtland, in Mather, Second Ann. Rept. Geol. Surv. Ohio, p. 190, footnote. Type locality: Ohio; type specimen: none designated.  
 1839. *Crotalus tergeminus* Sager, Senate Doc., State of Mich., p. 302.  
 1842. *Crotalophorus kirtlandi* Holbrook, N. Amer. Herpet., ed. 2, vol. 3, p. 31. Type locality: Ohio and Michigan; type specimen: none designated, but there are three catalogued as the types in the PANS collection, Nos. 7238, 7239, and 16662.  
 1853. *Crotalophorus tergeminus* Baird and Girard, Cat. N. Amer. Rept., part 1, p. 14.  
 1883. *Sistrurus catenatus* Garman, Mem. Mus. Comp. Zoöl., vol. 8, no. 3, pp. 118, 176.  
 1900. *Sistrurus catenatus catenatus* Cope, Rept. U. S. Nat. Mus. for 1898, p. 1146.

**Range:**—From central New York westward to Nebraska and Kansas, including: New York from Madison County west; southern Ontario along the shores of Georgian Bay, Lake Huron, and Lake Erie; also Prince Edward Peninsula in Lake Ontario; extreme western Pennsylvania; lower Michigan; northern and central Ohio and Indiana; Illinois; southern and southwestern Wisconsin; extreme southeastern Minnesota; central and southern Iowa; northern Missouri; extreme southeastern Nebraska; and extreme northeastern Kansas. Intergrades with *S. c. tergeminus* in the last two areas (fig. 2:10).

***Sistrurus catenatus edwardsii* (Baird and Girard)**

Desert Massasauga

Fig. 2:77

1853. *Crotalophorus edwardsii* Baird and Girard, Cat. N. Amer. Rept., part 1, p. 15. Type locality Tamaulipas, Mexico; type specimen: USNM 507.  
 1883. *Sistrurus miliaris* var. *edwardsii* Garman, Mem. Mus. Comp. Zoöl., vol. 8, no. 3, p. 177.  
 1892. *Crotalophorus catenatus edwardsii* Cope, Proc. U.S. Nat. Mus., vol. 14, p. 685.  
 1895. *Sistrurus catenatus edwardsii* Stejneger, Rept. U.S. Nat. Mus. for 1893, p. 416.  
 1936. *Sistrurus catenatus tergeminus* Klauber, Trans. S.D. Soc. Nat. Hist., vol. 8, no. 20, pp. 193, 229.  
 1955. *Sistrurus catenatus edwardsi* Gloyd, Bull. Chi. Acad. Sci., vol. 10, p. 84.

**Range:**—Texas, west of the Pecos River, together with the southern tip of the state; central and southern New Mexico; extreme southeastern Arizona; and probably extreme northern Tamaulipas, Mexico. The area of intergradation with *S. c. tergeminus* is broad, and there is uncertainty whether the massasaugas of the Texas Panhandle, and southeastern Colorado should be allocated to *edwardsii* or *tergeminus*. Tenta-

<sup>m</sup> See Science, vol. 19, no. 485, p. 290, May 20, 1892, for a discussion of this name and for the reasons for its validity despite the recency of its date of publication.

tively, in the present work, I have assigned them to the latter. Maslin (1965, p. 31) considers the Colorado specimens to be *edwardsii-tergeminus* intergrades. (fig. 2:10).

### ***Sistrurus catenatus tergeminus* (Say)**

Western Massasauga

Fig. 2:78

1823. *Crotalus tergeminus* Say, in Long's Exped. from Pittsburgh to Rocky Mts., edited by Edwin James, vol. 1, p. 499, footnote. Type locality: between the Mississippi River and the Rocky Mountains; type specimen: none designated. Type locality subsequently restricted to Winfield, Cowley County, Kansas, by Smith and Taylor, 1950, Univ. Kans. Sci. Bull., vol. 33, part 2, no. 8, p. 358.
1853. *Crotalophorus consors* Baird and Girard, Cat. N. Amer. Rept., part 1, p. 12. Type locality: Indianola, Texas; type specimen: USNM 512.
1883. *Sistrurus catenatus* var. *consors* Garman, Mem. Mus. Comp. Zoöl., vol. 8, no. 3, p. 176.
1936. *Sistrurus catenatus tergeminus* Klauber, Occ. Papers San Diego Soc. Nat. Hist., no. 1, p. 6.

*Range*:—The southwestern plains including: southeastern Nebraska; central and southwestern Kansas; extreme southeastern Colorado; northwestern Oklahoma; Texas between the Brazos and the Pecos rivers, excluding the extreme southern tip. Intergrades with *S. c. catenatus* in southeastern Nebraska and northeastern Kansas (fig. 2:10).

### ***Sistrurus miliarius miliarius* (Linné)**

Carolina Pigmy Rattlesnake

Fig. 2:79

1766. *Crotalus miliarius* Linné, Syst. Nat., ed. 12, p. 372. Type locality: Carolina; type specimen: received by Linné from Alexander Garden, disposition unknown.
1825. *Crotalophorus miliaris* Gray, Annals of Philos., n.s., vol. 10, art. 8, p. 205.
1826. *Caudisoma miliaria* Fitzinger, Neue Class. Rept., p. 63.
1883. *Sistrurus miliarius* Garman, Mem. Mus. Comp. Zoöl., vol. 8, no. 3, pp. 119, 177.
1935. *Sistrurus miliarius miliarius* Gloyd, Occ. Papers Mus. Zoöl. Univ. Mich., no. 322, p. 4.

*Range*:—From extreme southern South Carolina (where it intergrades with *S. m. barbouri*), north throughout South Carolina and eastern North Carolina to Hyde County. Also central Georgia and central Alabama (fig. 2:10).

### ***Sistrurus miliarius barbouri* Gloyd**

Dusky Pigmy Rattlesnake

Fig. 2:80

1819. *Crotalus miliarius* Say, Amer. Jour. Sci., vol. 1, p. 263.
1883. *Sistrurus miliarius* (part) Garman, Mem. Mus. Comp. Zoöl., vol. 8, no. 3, pp. 119, 177.
1935. *Sistrurus miliarius barbouri* Gloyd, Occ. Papers Mus. Zoöl. Univ. Mich., no. 322, p. 2. Type locality: Royal Palm Hammock, 12 miles west of Homestead, Dade County, Florida; type specimen: MCZ 12512.

*Range*:—From extreme southern South Carolina (where it intergrades with *S. m. miliarius*) and southern Georgia, south throughout Florida, and west across southern Alabama to southeastern Mississippi, intergrading with *S. m. streckeri* in the Pearl River Valley (fig. 2:10).

***Sistrurus miliarius streckeri* Gloyd**

**Western Pigmy Rattlesnake**

Fig. 2:81

1838. *Crotalus miliarius* (part) Holbrook, North Amer. Herp. [ed. 1], vol. 2, p. 73.  
 1883. *Sistrurus miliarius* (part) Garman, Mem. Mus. Comp. Zool., vol. 8, no. 3, pp. 119, 177.  
 1935. *Sistrurus miliarius streckeri* Gloyd, Occ. Papers Mus. Zool. Univ. Mich., no. 322, p. 4. Type locality: near Imboden, Lawrence County, Arkansas; type specimen: MZUM 76751.

*Range*:—From the Pearl River Valley of southern Mississippi and southeastern Louisiana (where it intergrades with *S. m. barbouri*), north and west through Mississippi, Louisiana, southwestern Tennessee, southern Missouri, Arkansas, southeastern Oklahoma, and eastern Texas (fig. 2:10). Probably present in northwestern Alabama.

***Sistrurus ravus* (Cope)**

**Mexican Pigmy Rattlesnake**

Fig. 2:82

1865. *Crotalus ravus* Cope, Proc. Acad. Nat. Sci. Phila., vol. 17, no. 4, p. 191. Type locality: tableland of Mexico; type specimens: USNM 25050–1. Type locality subsequently restricted to Totalco, Veracruz, by Smith and Taylor, 1950, Univ. Kans. Sci. Bull., vol. 33, part 2, no. 8, p. 351.  
 1896. *Sistrurus ravus* Boulenger, Cat. Snakes Brit. Mus., vol. 3, p. 571.

*Range*:—A small area of the Mexican plateau including: eastern and south-central México (state), Distrito Federal, Morelos, Tlaxcala, Puebla, west-central Veracruz, and central Oaxaca (fig. 2:10).

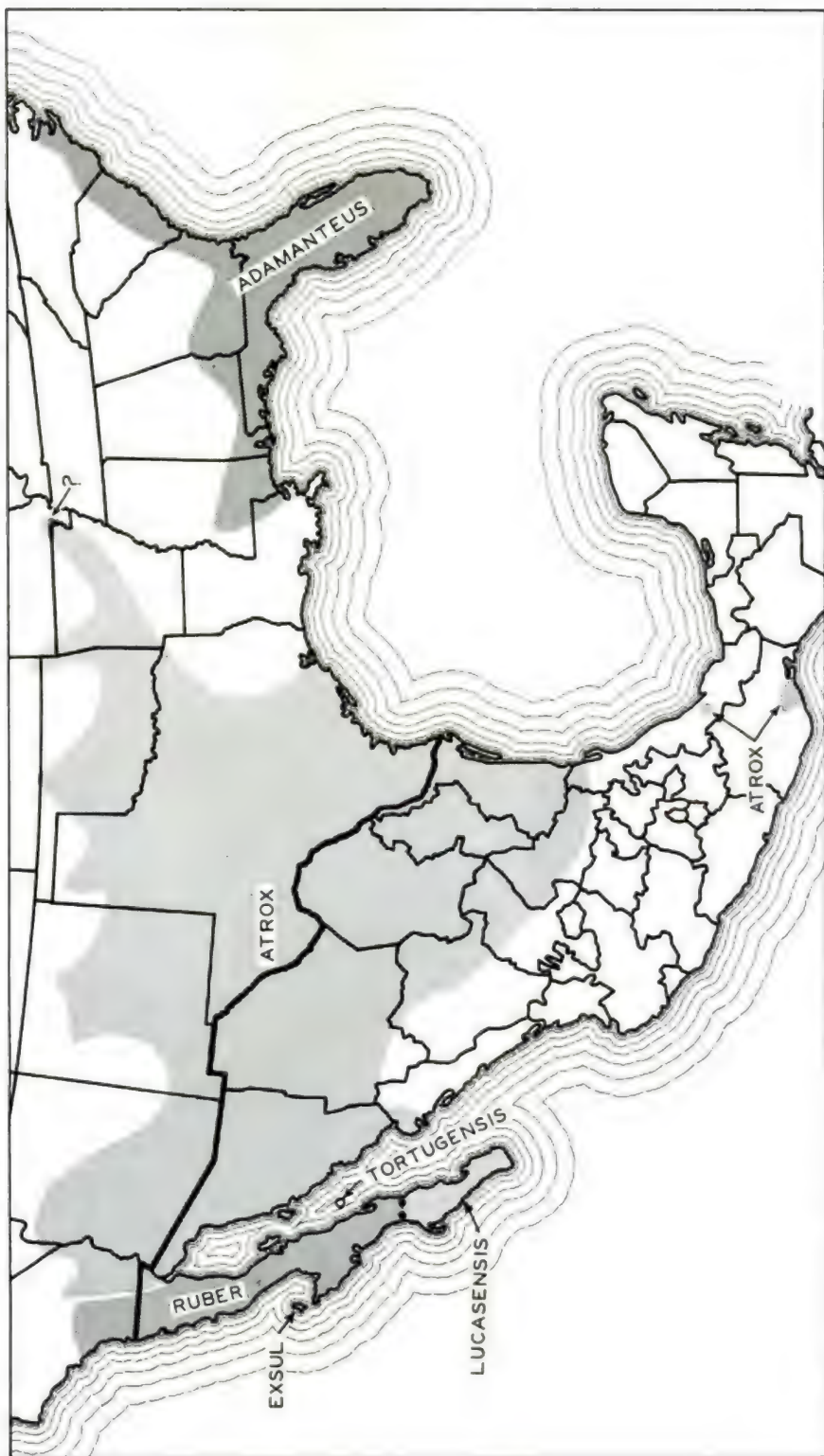


Fig. 2.1. Ranges of *C. adamanteus*, *C. atrox*, *C. exsul*, *C. ruber ruber*, *C. r. lucasensis*, and *C. tortugensis*.

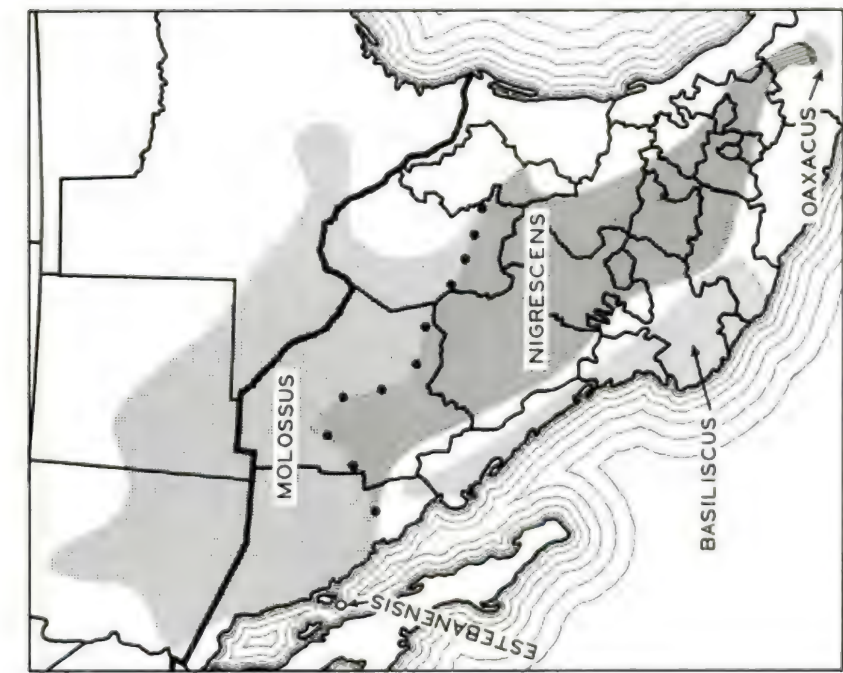


Fig. 2:2. Ranges of *C. basiliscus basiliscus*, *C. b. oaxacensis*, *C. molossus molossus*, *C. m. estebanensis*, and *C. m. nigrescens*. In this and subsequent maps, solid circles along boundaries between subspecies indicate areas of intergradation.

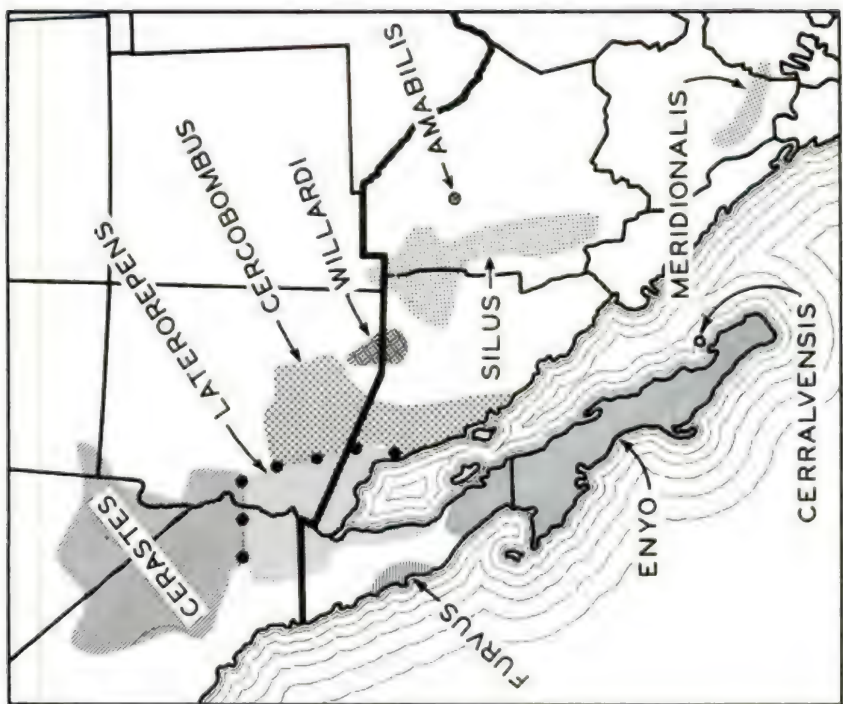


Fig. 2:3. Ranges of *C. cerastes cerastes*, *C. c. cercobombus*, *C. c. laterorrepens*, *C. enyo enyo*, *C. e. cerralvensis*, *C. e. furvus*, *C. willardi willardi*, *C. w. amabilis*, *C. w. meridionalis*, and *C. w. silus*.

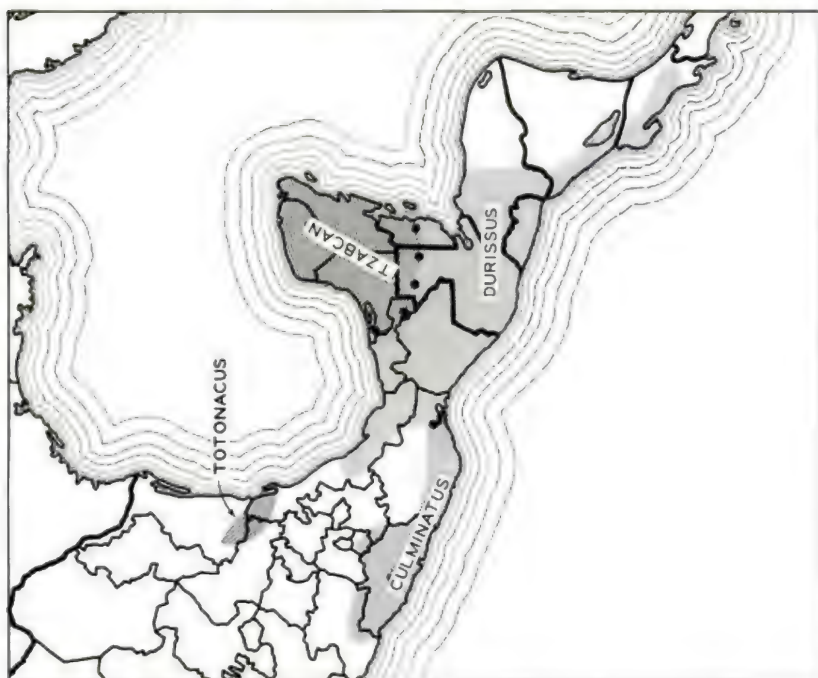


Fig. 2:4. Ranges of *C. durissus durissus*, *C. d. culminatus*, *C. d. totonacus*, and *C. d. tzabcan*.

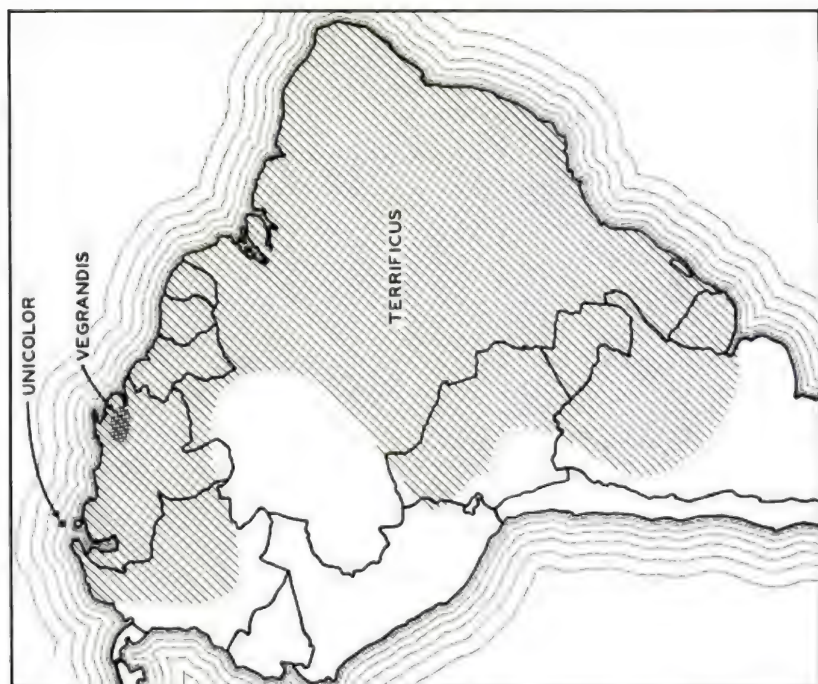


Fig. 2:5. Ranges of *C. durissus terrificus*, *C. unicolor*, and *C. uegrandis*.

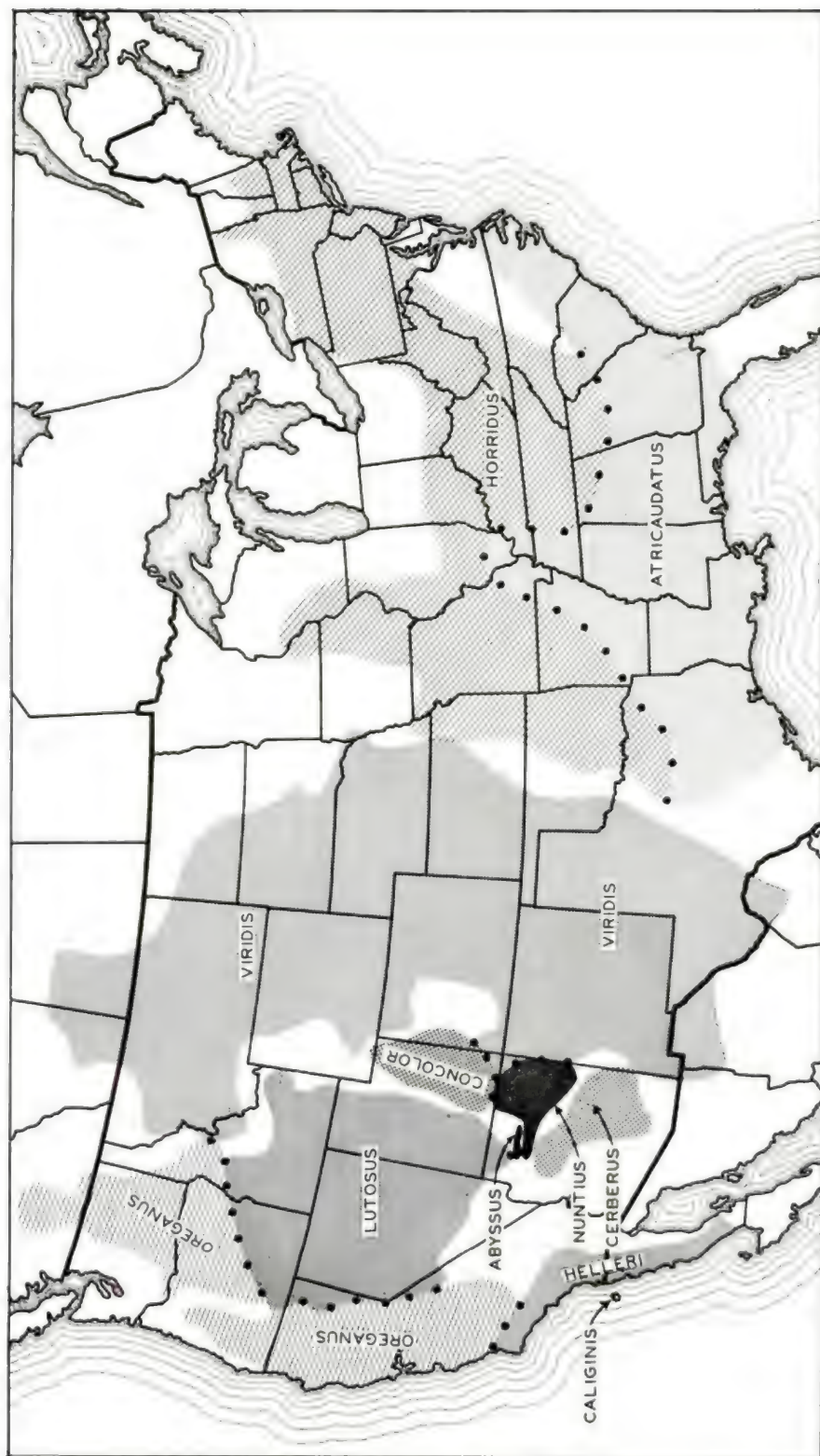


Fig. 2.6. Ranges of *C. horridus horridus*, *C. h. atricaudatus*, *C. viridis viridis*, *C. v. abyssus*, *C. v. caliginis*, *C. v. cerberus*, *C. v. concolor*, *C. v. helleri*, *C. v. lutosus*, *C. v. nuntius*, and *C. v. oregonus*.

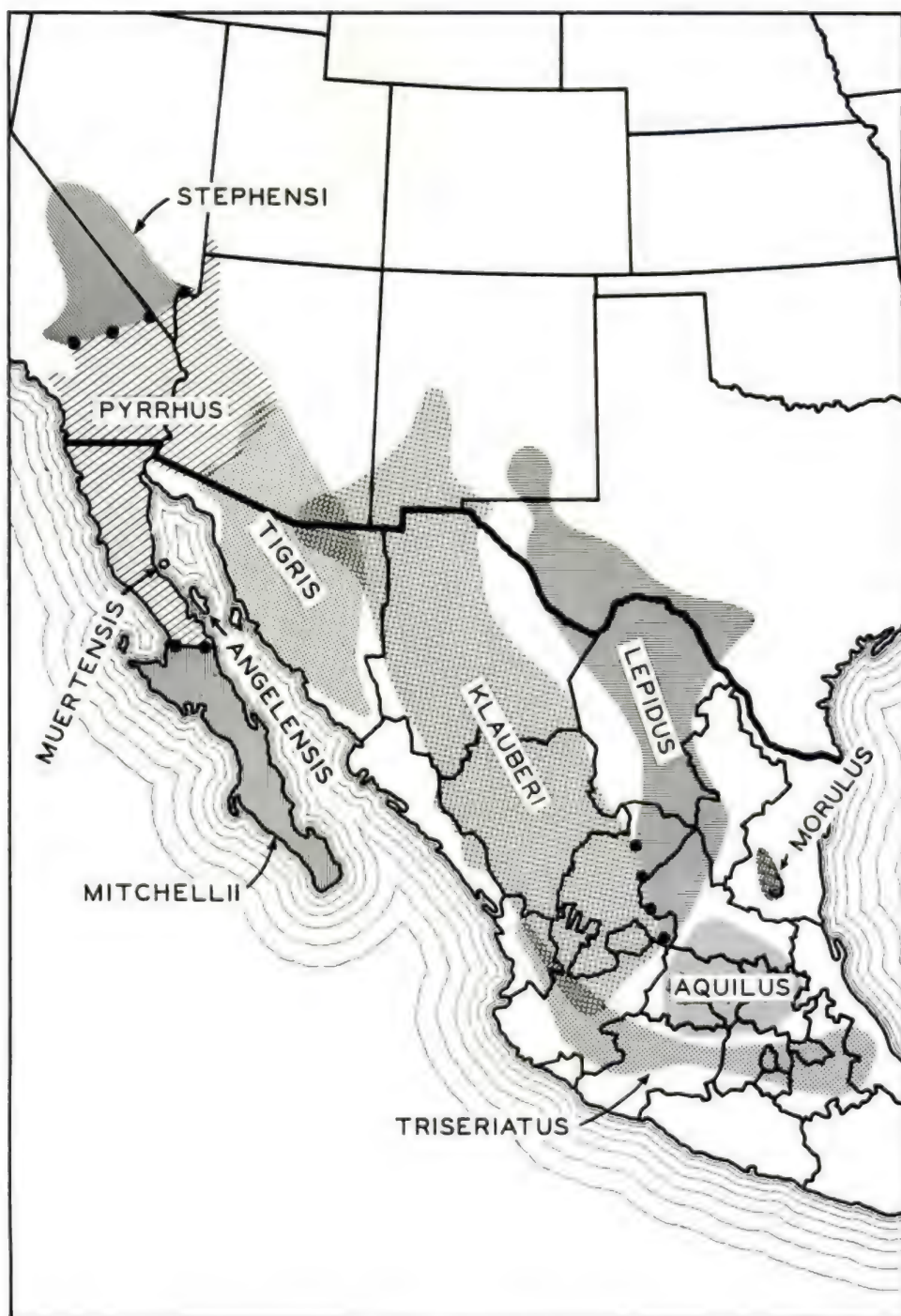


Fig. 2:7. Ranges of *C. lepidus lepidus*, *C. l. klauberi*, *C. l. morulus*, *C. mitchellii mitchellii*, *C. m. angelenus*, *C. m. muertensis*, *C. m. pyrrhus*, *C. m. stephensi*, *C. tigris*, *C. triseriatus triseriatus*, and *C. t. aquilus*.

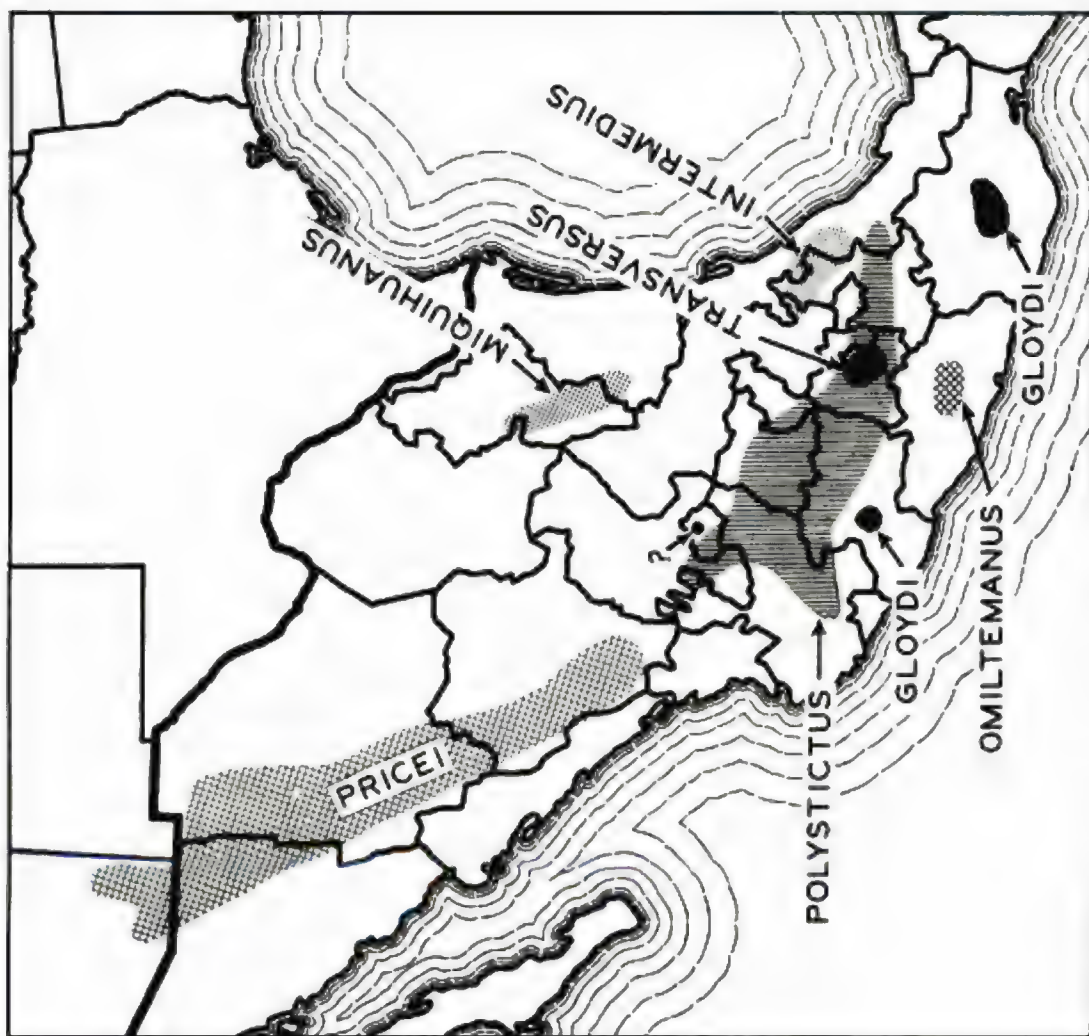


Fig. 2:8. Ranges of *C. intermedius intermedius*, *C. i. gloydi*, *C. i. omiltemanus*, *C. polystictus*, *C. pricei pricei*, *C. p. miquihuanus*, and *C. transversus*. The mark (?) represents a specimen allied to *C. pricei* but as yet subspecifically unallocated.

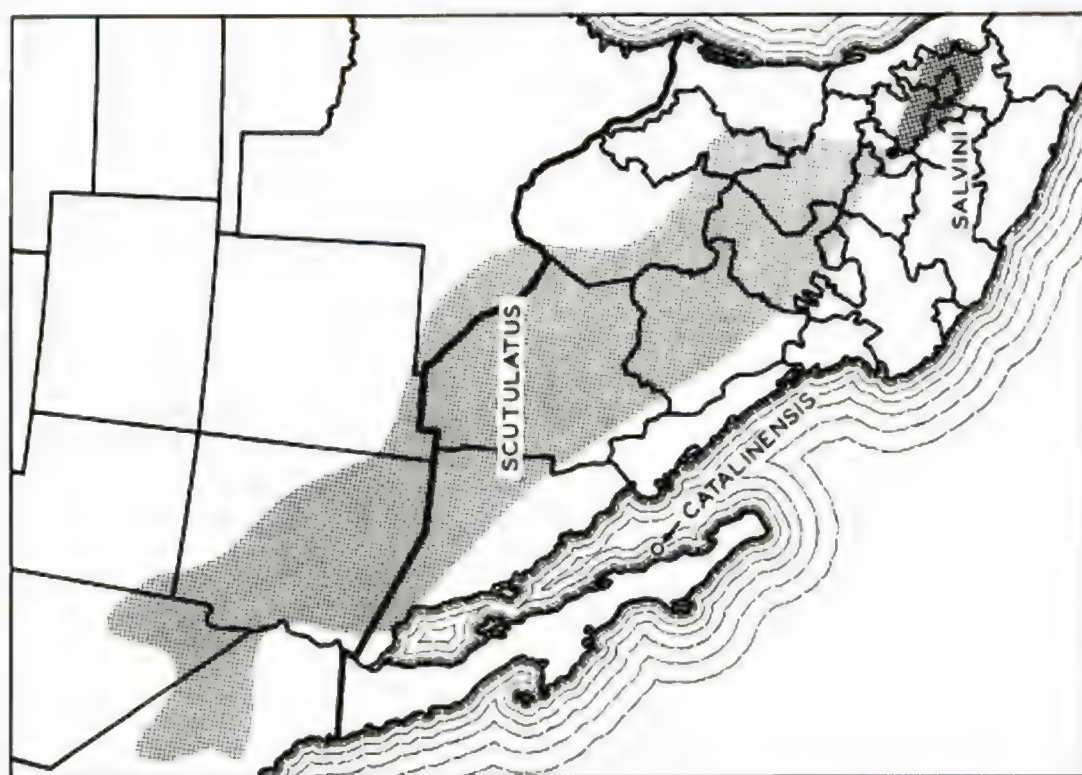


Fig. 2:9. Ranges of *C. catalinensis*, *C. scutulatus scutulatus*, and *C. s. salemi*.

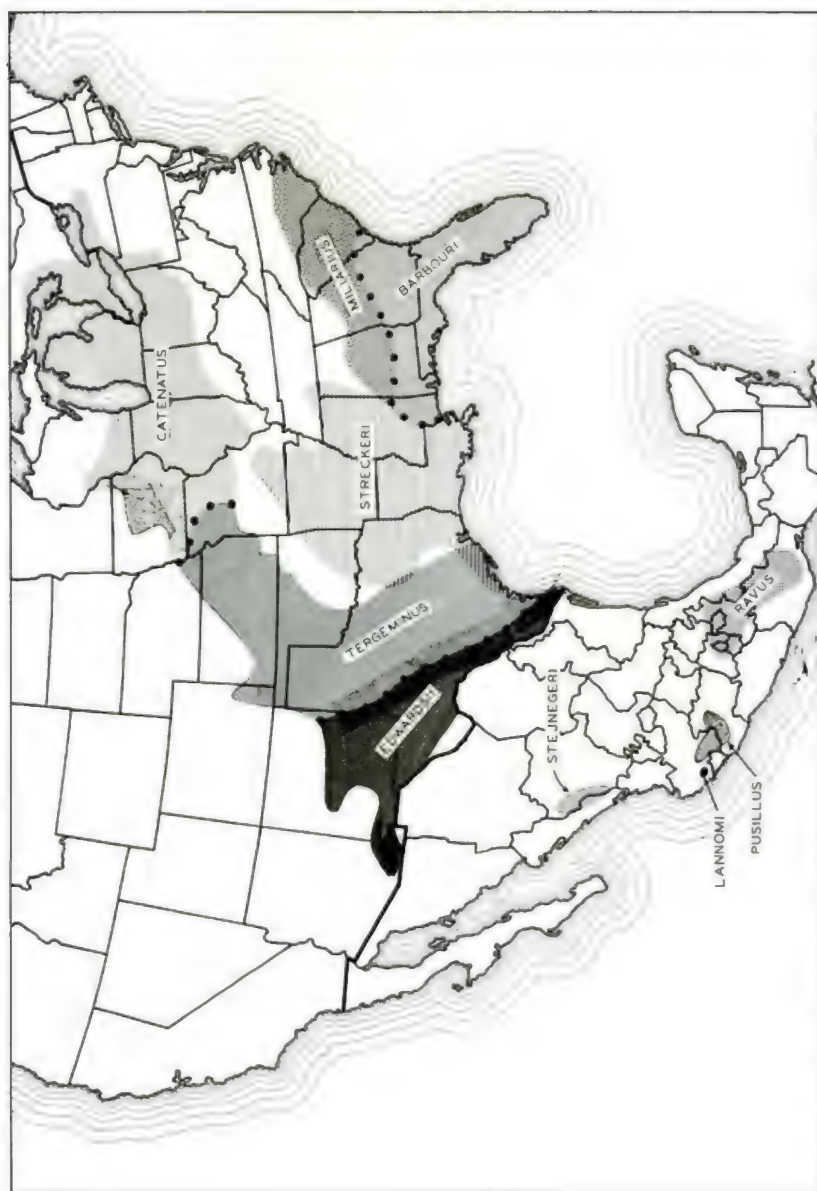


Fig. 2:10. Ranges of *C. lannomi*, *C. pusillus*, *C. stejnegeri*, *S. catenatus catenatus*, *S. c. edwardsi*, *S. c. tergeninus*, *S. m. barbouri*, *S. m. streckeri*, and *S. ravus*.

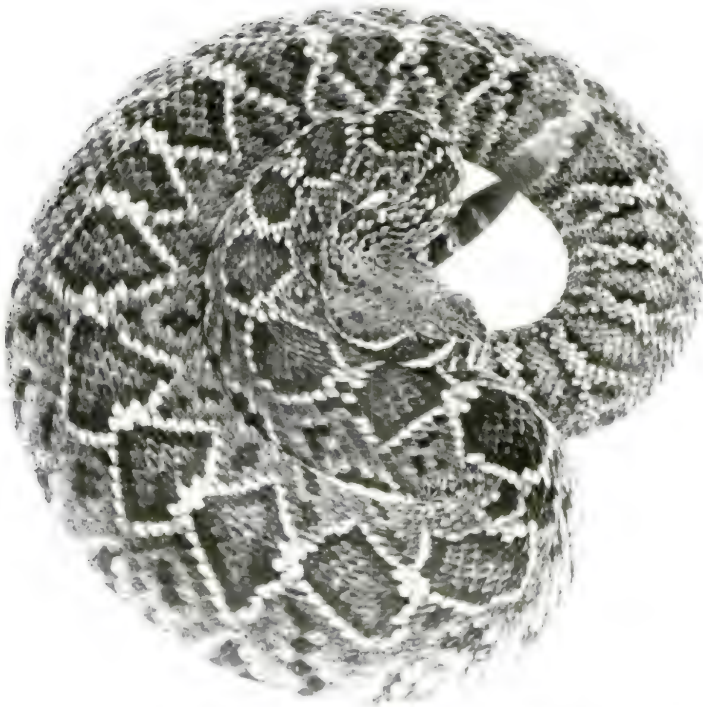


Fig. 2:11. *Crotalus adamanteus*, Eastern Diamondback Rattlesnake. (Specimen from Eureka, Marion County, Florida. The blur at the tail is the vibrating rattle.)



Fig. 2:12. *Crotalus atrox*, Western Diamondback Rattlesnake. (Specimen from Date, Yavapai County, Arizona.)

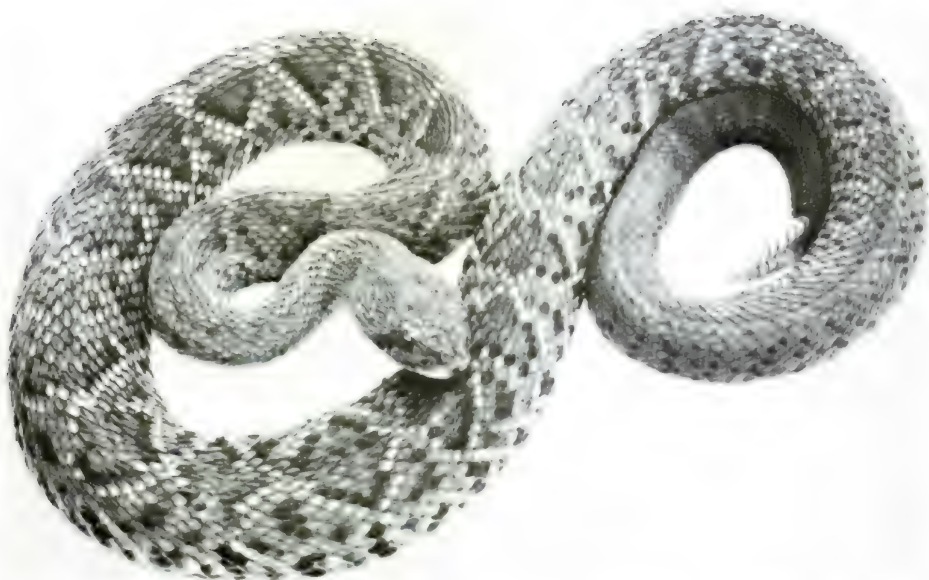


Fig. 2:13. *Crotalus basiliscus basiliscus*, Mexican West-Coast Rattlesnake. (Specimen from near Colima, Colima, Mexico.)



Fig. 2:14. *Crotalus basiliscus oaxacus*, Oaxacan Rattlesnake. (Specimen from near San Bartolo Coyotepec, Oaxaca, Mexico. Photograph courtesy of C. M. Bogert, The American Museum of Natural History, N.Y.)



Fig. 2:15. *Crotalus catalinensis*, Santa Catalina Island or Rattleless Rattlesnake. (Specimen from Santa Catalina Island, Gulf of California, Mexico. Photograph by R. Van Nostrand.)



Fig. 2:16. *Crotalus cerastes cerastes*, Mojave Desert Sidewinder. (Specimen from near Kramer Junction, San Bernardino County, California.)



Fig. 2:17 *Crotalus cerastes cercobombus*, Sonoran Desert Sidewinder. (Specimen from near Marana, Pima County, Arizona.)



Fig. 2:18. *Crotalus cerastes laterorepens*, Colorado Desert Sidewinder. (Specimen from Borrego Valley, San Diego County, California.)



Fig. 2:19. *Crotalus durissus durissus*, Central American Rattlesnake. (Specimen from near Veracruz, Veracruz, Mexico.)



Fig. 2:20. *Crotalus durissus culminatus*, Northwestern Neotropical Rattlesnake. (Specimen from near Izucar de Matamoros, Puebla, Mexico, furnished by Ray Folsom. Photograph by R. Van Nostrand.)



Fig. 2:21. *Crotalus durissus terrificus*, South American Rattlesnake. (Specimen from Central Brazil. Photograph by courtesy of the New York Zoological Society.)



Fig. 2:22. *Crotalus durissus terrificus*, South American Rattlesnake. (Specimen from near Barranquilla, Colombia.)

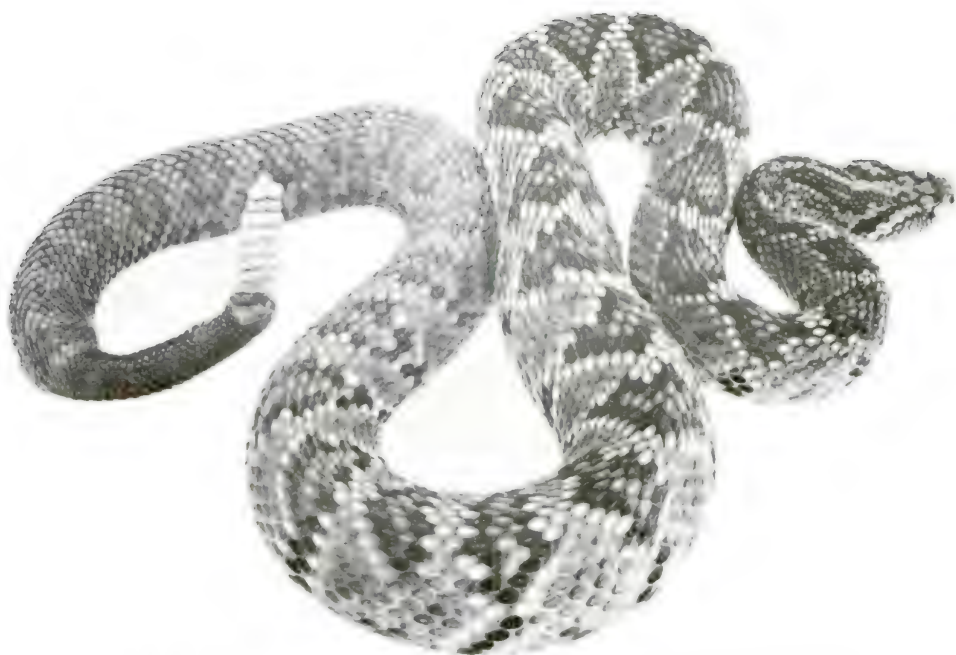


Fig. 2:23. *Crotalus durissus totonacus*, Totonacan Rattlesnake. (Specimen from an unknown locality.)



Fig. 2:24. *Crotalus durissus tzabcan*, Yucatán Neotropical Rattlesnake. (Specimen from Mérida, Yucatán, Mexico, furnished by Ray Folsom. Photograph by R. Van Nostrand.)



Fig. 2:25. *Crotalus enyo enyo*, Lower California Rattlesnake. (Specimen from La Rivera, Baja California del Sur, Mexico.)



Fig. 2:26. *Crotalus enyo cerraluensis*, Cerralvo Island Rattlesnake. (Specimen from Cerralvo Island, Gulf of California, Mexico, furnished by Dr. George E. Lindsay, California Academy of Sciences, San Francisco. Photograph by Dallas Clites.)

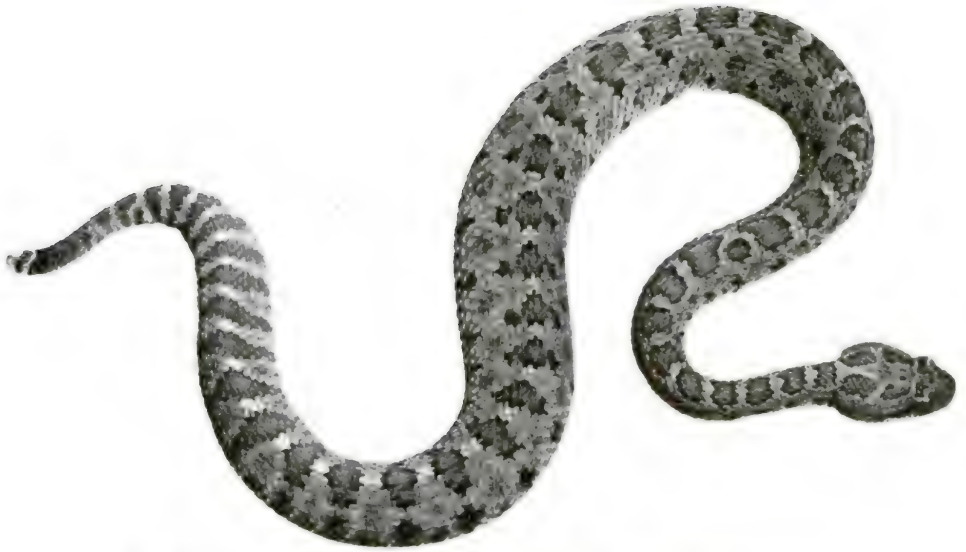


Fig. 2:27. *Crotalus enyo ferox*, Rosario Rattlesnake. (Specimen from near El Rosario, Baja California del Norte, Mexico.)



Fig. 2:28. *Crotalus enyo ferox*, Rosario Rattlesnake. (Specimen from near Camalu, Baja California del Norte, Mexico; furnished by Dennis L. Bostic. San Diego Zoo Photo by Ron Garrison.)



Fig. 2:29. *Crotalus exsul*, Cedros Island Diamond Rattlesnake. (Specimen from Cedros Island, Pacific Coast of Baja California, Mexico.)



Fig. 2:30. *Crotalus horridus horridus*, Timber Rattlesnake. (Specimen from near Baraboo, Sauk County, Wisconsin.)



Fig. 2:31. *Crotalus horridus atricaudatus*, Canebrake Rattlesnake. (Specimen from Imboden, Lawrence County, Arkansas.)



Fig. 2:32. *Crotalus intermedius intermedius*, Totalcan Small-Headed Rattlesnake. (Specimen from near Las Vigas, Veracruz, Mexico. Photograph courtesy of E. D. Keiser, Jr., Louisiana State University.)



Fig. 2:33. *Crotalus intermedius gloydi*, Oaxacan Small-Headed Rattlesnake. (Specimen from 6 miles south of Tyocote, Oaxaca, Mexico. Photograph courtesy of C. M. Bogert, The American Museum of Natural History, N.Y.)

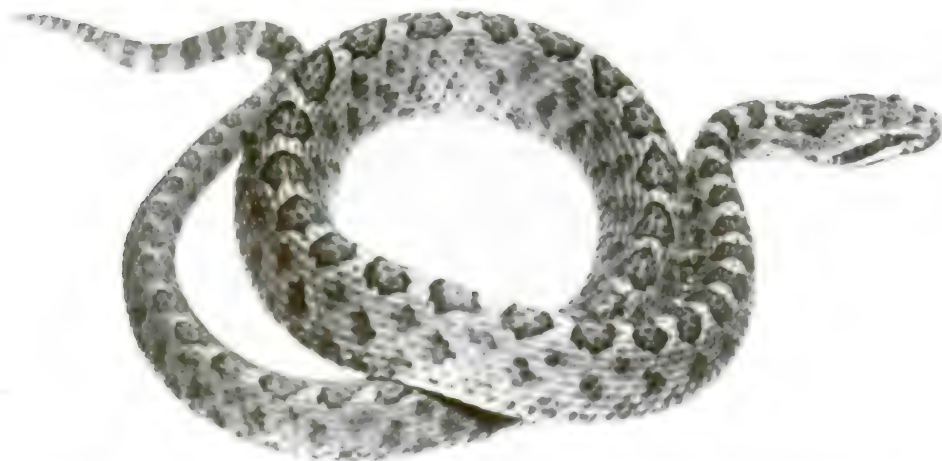


Fig. 2:34. *Crotalus intermedius omiltemanus*, Omilteman Small-Headed Rattlesnake. (Specimen from near Omilteme, Guerrero, Mexico.)

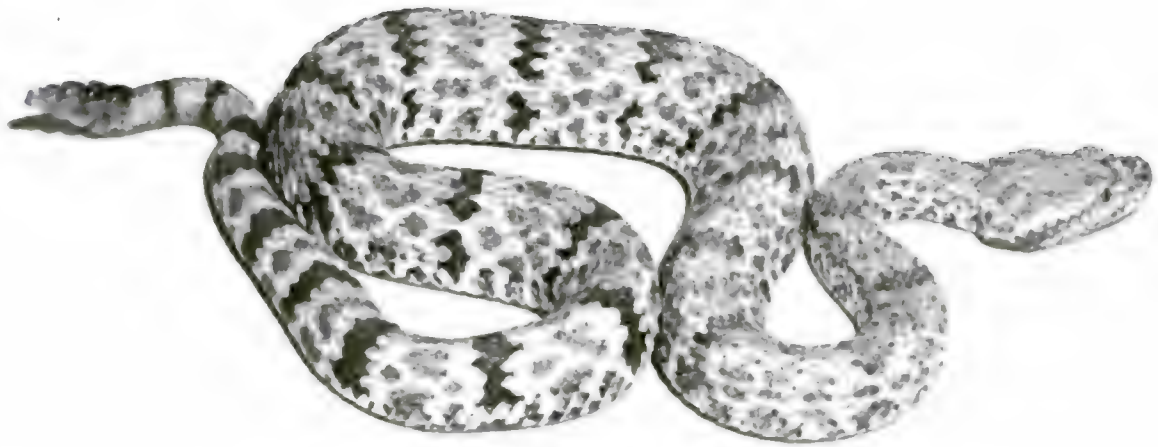


Fig. 2:35. *Crotalus lepidus lepidus*, Mottled Rock Rattlesnake. (Specimen from 10 miles southwest of Leakey, Real County, Texas. Photograph by Isabelle H. Conant, published by courtesy of Roger Conant, Philadelphia Zoölogical Society.)



Fig. 2:36. *Crotalus lepidus klauberi*, Banded Rock Rattlesnake. (Specimen from Gold Gulch, Dos Cabezas Mountains, Cochise County, Arizona.)



Fig. 2:37. *Crotalus lepidus klauberi*, Banded Rock Rattlesnake. (Specimen from near Mimbres, Grant County, New Mexico.)



Fig. 2:38. *Crotalus mitchellii mitchellii*, San Lucan Speckled Rattlesnake. (Specimen from La Rivera, Baja California del Sur, Mexico.)



Fig. 2:39. *Crotalus mitchellii angelensis*, Angel de la Guarda Island Speckled Rattlesnake. (Specimen from Angel de la Guarda Island, Gulf of California, Mexico. Photograph by Ron Garrison.)



Fig. 2:40. *Crotalus mitchellii muertensis*, El Muerto Island Speckled Rattlesnake. (Specimen from El Muerto Island, San Luis group, Gulf of California, Mexico.)



Fig. 2:41. *Crotalus mitchellii pyrrhus*, Southwestern Speckled Rattlesnake. (Specimen from Yaqui Well, San Diego County, California.)



Fig. 2:42. *Crotalus mitchellii stephensi*, Panamint Rattlesnake. (Specimen from Aberdeen, Inyo County, California.)

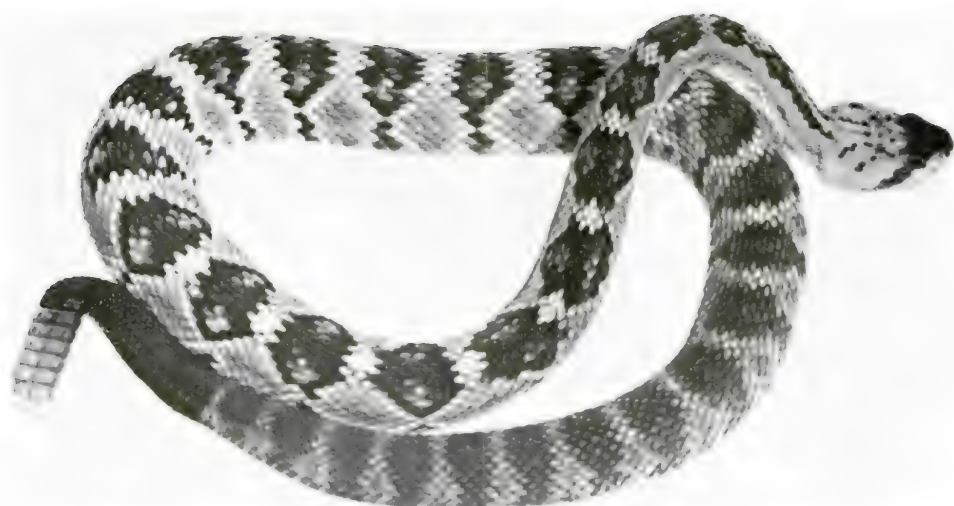


Fig. 2:43. *Crotalus molossus molossus*, Northern Black-Tailed Rattlesnake. (Specimen from Ramsey Canyon, Huachuca Mountains, Cochise County, Arizona.)



Fig. 2:44. *Crotalus molossus estebanensis*, San Esteban Island Rattlesnake. (Specimen from San Esteban Island, Gulf of California, Mexico.)



Fig. 2:45. *Crotalus molossus nigrescens*, Mexican Black-Tailed Rattlesnake.  
(Specimen from near Yamoriba, Durango, Mexico.)



Fig. 2:46. *Crotalus polystictus*, Mexican Lance-headed Rattlesnake. (Specimen from south-eastern Jalisco, Mexico, furnished by R. Terry Basey and Barry L. Armstrong. San Diego Zoo Photo by Ron Garrison.)



Fig. 2:47. *Crotalus pricei pricei*, Western Twin-Spotted Rattlesnake. (Specimen from San José de Babicora, Chihuahua, Mexico.)

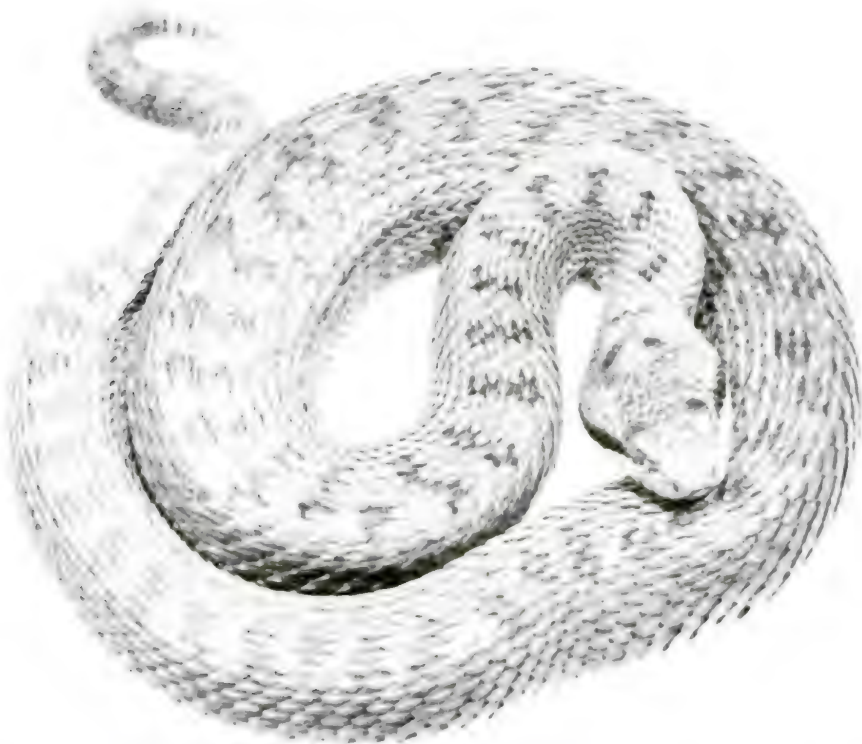


Fig. 2:48. *Crotalus pricei miquihuanus*, Eastern Twin-Spotted Rattlesnake. (Specimen from Sierra de los Amargos, Coahuila, Mexico. Photograph courtesy of Dr. R. W. Axtell.)



Fig. 2:49. *Crotalus pusillus*, Tancitaran Dusky Rattlesnake. (Specimen from Dos Aguas, Michoacán, Mexico. Photograph courtesy of Dr. W. E. Duellman.)



Fig. 2:50. *Crotalus ruber ruber*, Red Diamond Rattlesnake (coastal phase). (Specimen from Santa Margarita, San Diego County, California.)

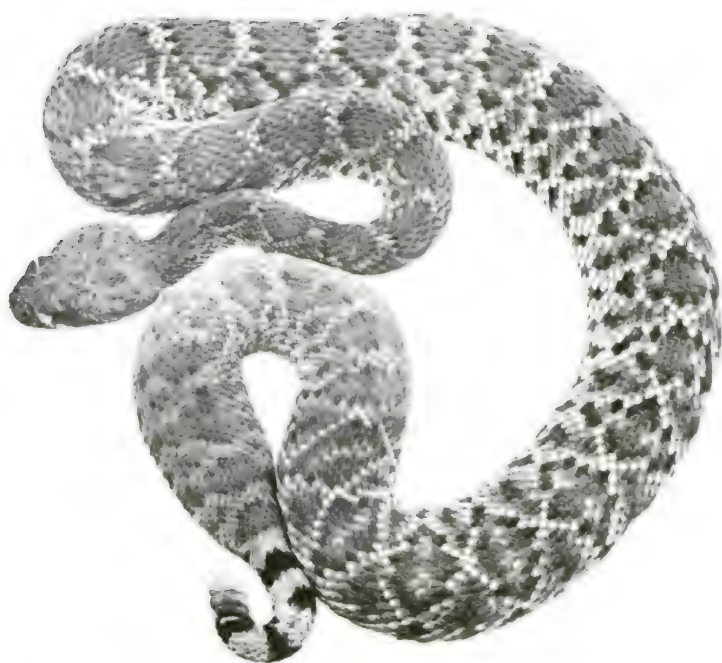


Fig. 2:51. *Crotalus ruber ruber*, Red Diamond Rattlesnake (desert phase).  
(Specimen from near Vallecito, San Diego County, California.)

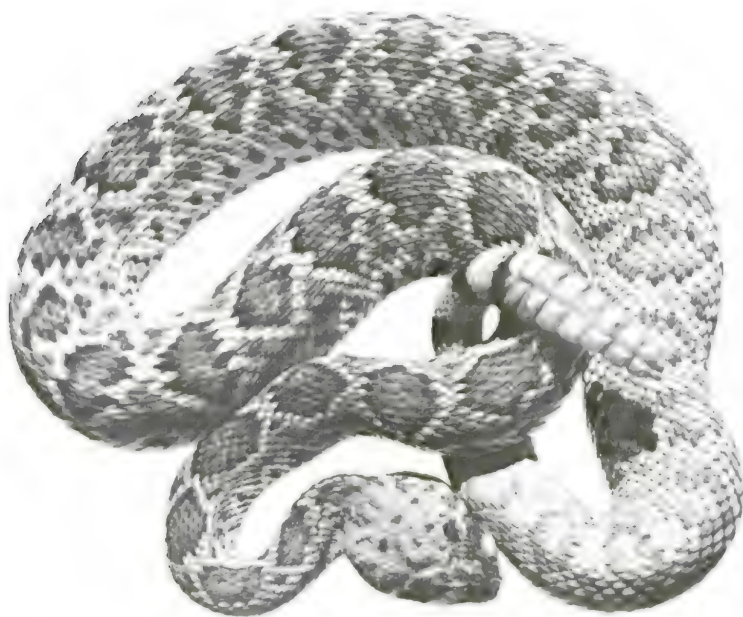


Fig. 2:52. *Crotalus ruber lucasensis*, San Lucan Diamond Rattlesnake.  
(Specimen from La Rivera, Baja California del Sur, Mexico.)



Fig. 2:53. *Crotalus scutulatus scutulatus*, Mojave Rattlesnake. (Specimen from Date Creek, Yavapai County, Arizona.)



Fig. 2:54. *Crotalus scutulatus salvini*, Huamantlan Rattlesnake. (Specimen from near Totalco, Veracruz, Mexico. Photograph courtesy of R. Terry Basey.)



Fig. 2:55. *Crotalus stejnegeri*, Long-Tailed Rattlesnake. (Specimen from near Yamoriba, Durango, Mexico.)

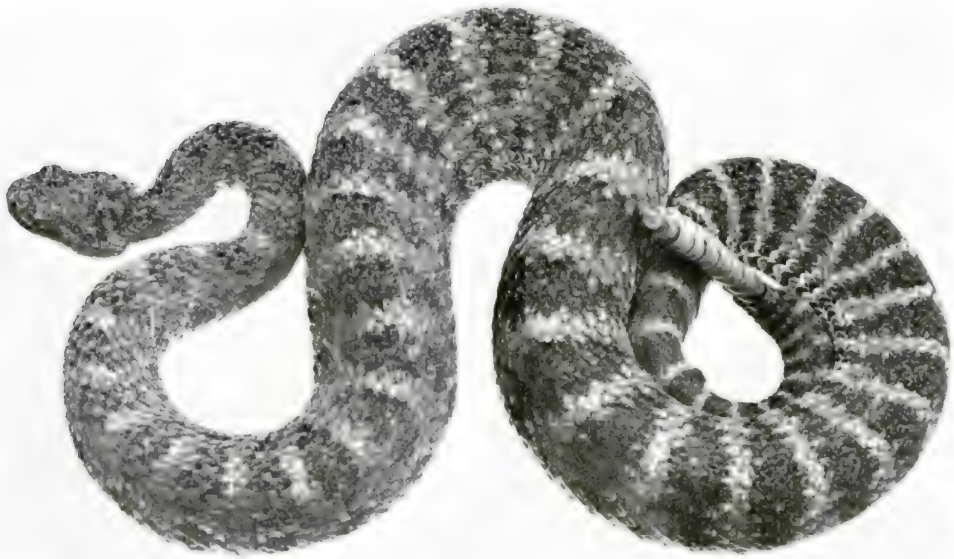
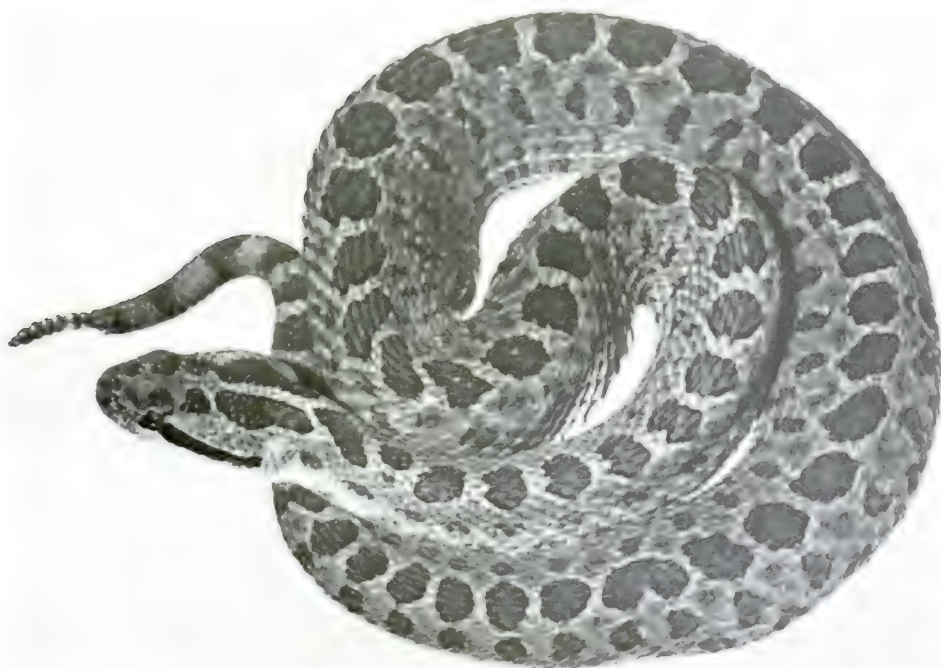


Fig. 2:56. *Crotalus tigris*, Tiger Rattlesnake. (Specimen from Estrella Mountains, Maricopa County, Arizona.)



**Fig. 2:57.** *Crotalus tortugensis*, Tortuga Island Diamond Rattlesnake. (Specimen from Tortuga Island, Gulf of California, Mexico.)



**Fig. 2:58.** *Crotalus triseriatus triseriatus*, Central-Plateau Dusky Rattlesnake. (Specimen from near Tres Cumbres, Morelos, Mexico.)



Fig. 2:59. *Crotalus triseriatus aquilus*, Queretaran Dusky Rattlesnake.  
(Specimen from Jacala, Hidalgo, Mexico.)



Fig. 2:60. *Crotalus unicolor*, Aruba Island Rattlesnake. (Specimen from  
Aruba Island, off the coast of Venezuela.)

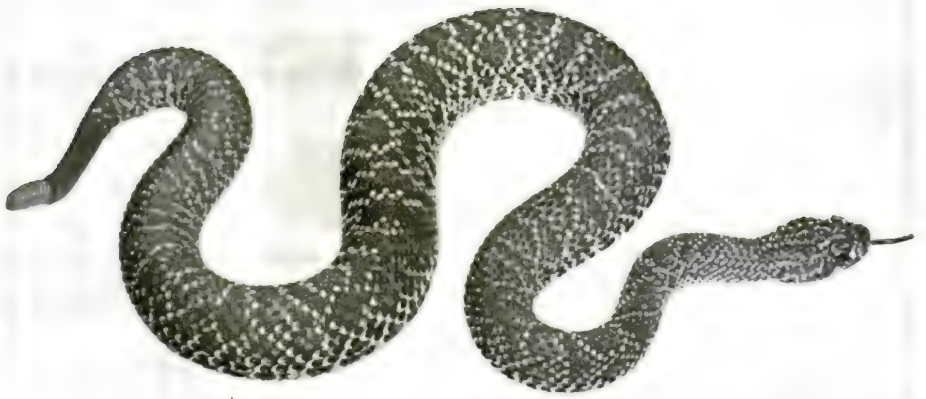


Fig. 2:61. *Crotalus vegrandis*, Uracoan Rattlesnake. (Specimen from Sabanas de Uracoa, Distrito Sotillo, State of Monagas, Venezuela, furnished by Dr. A. R. Lancini. Photograph by Ron Garrison.)



Fig. 2:62. *Crotalus viridis viridis*, Prairie Rattlesnake. Specimen from near Jetmore, Hodgeman County, Kansas.)

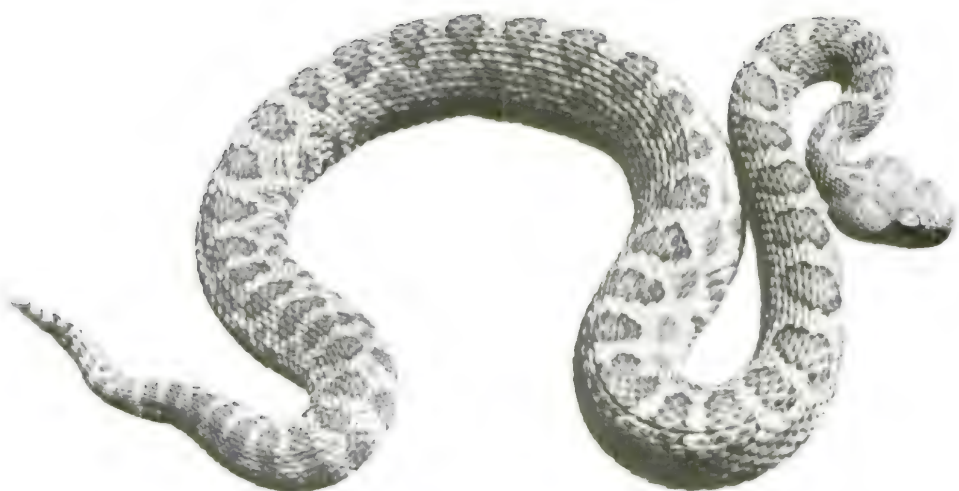


Fig. 2:63. *Crotalus viridis abyssus*, Grand Canyon Rattlesnake. (Specimen from the North Rim of the Grand Canyon, Coconino County, Arizona.)

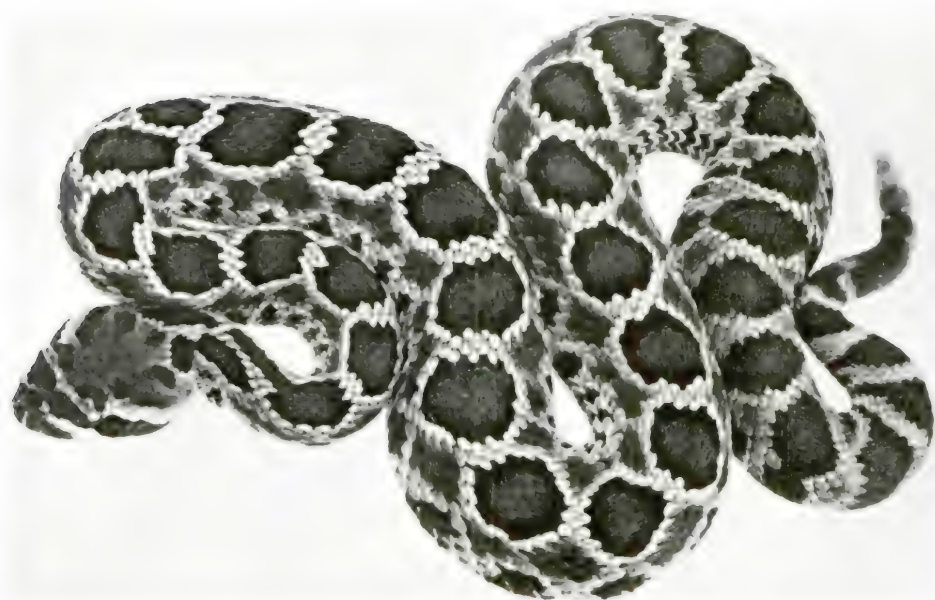


Fig. 2:64. *Crotalus viridis caliginis*, Coronado Island Rattlesnake. (Specimen from South Coronado Island, northwest coast of Baja California del Norte, Mexico.)



Fig. 2:65. *Crotalus viridis cerberus*, Arizona Black Rattlesnake. (Specimen from Hillside, Yavapai County, Arizona.)



Fig. 2:66. *Crotalus viridis concolor*, Midget Faded Rattlesnake. (Specimen from Jensen, Uintah County, Utah.)



Fig. 2:67. *Crotalus viridis helleri*, Southern Pacific Rattlesnake. (Specimen from Rancho Santa Fe, San Diego County, California.)



Fig. 2:68. *Crotalus viridis lutosus*, Great Basin Rattlesnake. (Specimen from near Boise, Idaho.)



Fig. 2:69. *Crotalus viridis nuntius*, Hopi Rattlesnake. (Specimen from Canyon Padre, Coconino County, Arizona.)



Fig. 2:70. *Crotalus viridis oreganus*, Northern Pacific Rattlesnake. (Specimen from near Wenatchee, Chelan County, Washington.)

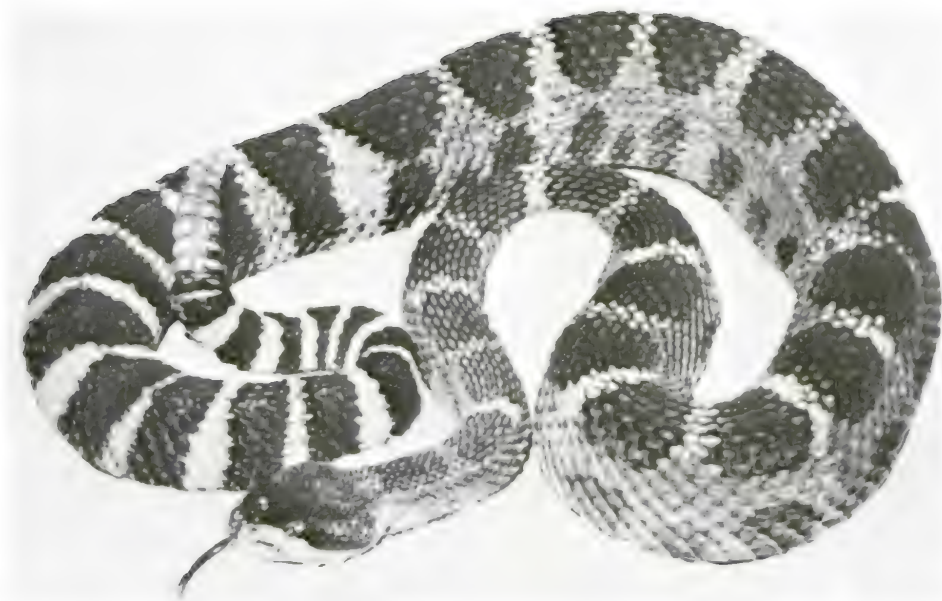


Fig. 2:71. *Crotalus viridis oreganus*. (Specimen probably from Trinity County, California. Photograph courtesy of J. H. Tashjian.)



Fig. 2:72. *Crotalus willardi willardi*, Arizona Ridge-Nosed Rattlesnake. (Specimen from Ramsey Canyon, Huachuca Mountains, Cochise County, Arizona.)



Fig. 2:73. *Crotalus willardi amabilis*, Del Nido Ridge-Nosed Rattlesnake. (Specimen from Arroyo Mesteño, Sierra del Nido, Chihuahua, Mexico. Photograph courtesy of J. D. Anderson and G. M. Christman.)



Fig. 2:74. *Crotalus willardi meridionalis*, Southern Ridge-Nosed Rattlesnake. (Specimen from Durango, Mexico, collected by Dr. R. W. Axtell. Photograph courtesy of J. E. Werler, Houston Zoological Gardens.)



Fig. 2:75 *Crotalus willardi silus*, West Chihuahuan Ridge-Nosed Rattlesnake. (Specimen from Indian Creek Canyon, near Animas Peak, Hidalgo County, New Mexico. Photograph courtesy of C. M. Bogert, The American Museum of Natural History, N. Y.)



Fig. 2:76. *Sistrurus catenatus catenatus*, Eastern Massasauga. The flattening of the body is a defensive reaction. (Specimen from Proud Lake, Oakland County, Michigan.)





Fig. 2:79. *Sistrurus miliarius miliarius*, Carolina Pigmy Rattlesnake. (Specimen Leesville, Lexington County, South Carolina. Photograph courtesy of Dr. Howard K. Gloyd, University of Arizona.)



Fig. 2:80. *Sistrurus miliarius barbouri*, Dusky Pigmy Rattlesnake. (Specimen from Marion County, Florida.)



Fig. 2:81. *Sistrurus miliarius streckeri*, Western Pigmy Rattlesnake. (Specimen from Gentilly, Orleans Parish, Louisiana.)



Fig. 2:82. *Sistrurus ravus*, Mexican Pigmy Rattlesnake. (Specimen from near Huitzilas, Morelos, Mexico. Photograph courtesy J. E. Werler, Houston Zoölogical Gardens.)

# CONDENSED ALPHABETICAL SYNONYMY OF THE RATTLESNAKES

I shall omit from this condensed alphabetical synonymy of the rattlesnakes, in which all the proposed generic, specific, and subspecific names have been included regardless of their validity, such obvious misspellings and unwarranted emendations as *trigeminus* of Lichtenstein and von Martens, 1856, p. 34; *oregonensis* of Boulenger, 1896, Cat. vol. 3, p. 580; *articanatus*, *cincolor*, *dorissus*, *catesbyanum*, *massasauga*, and *tergemia* of Notestein, 1905, pp. 123, 125; and *scutellatus* of Stejneger and Barbour, 1939, Check List, ed. 4, p. 150. I have also ignored *C. albus*, *C. fasciatus*, and *C. tertius* of Kerr, 1802, vol. 4, pp. 282-284. Kerr, in certain footnotes, cites these names as if they had previously been used binominally by Boddaert, Vosmaer, and Gronovius. However, this was not the case; they were merely abbreviated references to certain nonbinominal descriptions made by these earlier authors.

I have ignored (with the exception of his *Crotalus fasciatus*) the fantastic nomenclatorial results produced by Higgins (1873, p. 74), who placed a large number of Asiatic forms in the genus *Crotalus*, under the species *C. trimeresurus*, *C. peltopelor*, *C. halys*, and *C. hypnale*. Higgins had a confused knowledge of the rules of nomenclature and the scope of the different grades of classification, which rendered his names unworthy of notice.

I have not included two humorous *nomina nuda*: *Crotalus nocturnus* ("Packer Joe" in Calico Print, vol. 7, no. 2, p. 3, Feb., 1952), and *Crotalus cerastes visaversus* ("R. A. Tell" in Calico Print, vol. 8, no. 5, p. 35, June, 1952).

Minor emendations (e.g., *oregonus* for *oreganus*) are not considered to warrant separate entries.

Where the application or allocation of a name requires an explanation, such explanation will be found in the Check List.

The synonymy follows:

- abyssus* Klauber, 1930. Valid subspecies of *C. viridis*.
- adamanteus* Beauvois, 1799. Valid species in the genus *Crotalus*.
- Æchmophrys* Coues, 1875. Synonym of *Crotalus*.
- albicans* D'Amour, Becker, and Van Riper, 1936. *Nomen nudum*, intended to indicate *C. v. viridis*.
- amabilis* Anderson, 1962. Valid subspecies of *C. willardi*.
- americana* Catesby, 1743. Pre-Linnean *nomen nudum*.
- anahuacus* Gloyd, 1940. Synonym of *C. t. triseriatus*.
- angelensis* Klauber, 1963. Valid subspecies of *C. mitchellii*.
- aquilus* Klauber, 1952. Valid subspecies of *C. triseriatus*.
- Aploaspis* Cope, 1866. Synonym of *Crotalus*.
- atricaudatus* Latreille, 1802. Valid subspecies of *C. horridus*.
- atrox* Baird and Girard, 1853. Valid species in the genus *Crotalus*.
- barbouri* Gloyd, 1935. Valid subspecies of *S. miliarius*.
- basiliscus* Cope, 1864. Valid species in the genus *Crotalus*.
- boiquira* Lacépède, 1789. Synonym of *C. horridus*, probably of the subspecies *C. h. horridus*.
- caliginis* Klauber, 1949. Valid subspecies of *C. viridis*.
- cascavella* Wagler in Spix, 1821. Synonym of *C. d. terrificus*, but see footnote 8 under *C. d. terrificus* in the Check List.
- catalinensis* Cliff, 1954. Valid species in the genus *Crotalus*.
- catenatus* Rafinesque, 1818. Valid species in the genus *Sistrurus*.
- catesbaei* Hemprich, 1820. Synonym of *C. h. atricaudatus*.
- Caudisona* Laurenti, 1768. Synonym of *Crotalus*.

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- caudisona* Wheatley, 1886 (specific name). *Nomen nudum*, to be considered a synonym of *C. h. horridus*.
- cerastes* Hallowell, 1854. Valid species of the genus *Crotalus*.
- cerberus* Coues, 1875. Valid subspecies of *C. viridis*.
- cercobombus* Savage and Cliff, 1953. Valid subspecies of *C. cerastes*.
- cerraltvensis* Cliff, 1954. Valid subspecies of *C. enyo*.
- cinereus* Le Conte, in Hallowell, 1852. Synonym of *C. atrox*. See footnote 2 under *C. atrox* in Check List.
- collilineatus* Amaral, 1926. Synonym of *C. d. terrificus*.
- collirhombeatus* Amaral, 1926. Synonym of *C. d. terrificus*.
- concolor* Jan, 1859. Synonym of *C. h. horridus*. *Concolor* Jan, 1859, was suppressed by the International Commission in Opinion 339.
- concolor* Woodbury, 1929. Valid subspecies of *C. viridis*.
- confluentus* Say, 1823. Synonym of *C. viridis*.
- consors* Baird and Girard, 1853. Synonym of *S. c. tergeminus*.
- copeanus* Amaral, 1937. *Nomen nudum*. Fixed in the synonymy of *C. d. durissus* by Gloyd, 1940.
- Crotalinus* Rafinesque, 1818. Synonym of *Crotalus*.
- Crotalophorus* Houttuyn, 1761. Synonym of *Crotalus*.
- crotalurus* Rafinesque, 1820. Synonym of *Crotalus*.
- Crotalus* Linné, 1758. Valid name of one of the two genera of rattlesnakes. Type species: *C. horridus*.
- crotaminicus* Moura Gonçalves, 1960. *Nomen nudum*. See footnote 8 under *terrificus* in the Check List.
- culminatus* Klauber, 1952. Valid subspecies of *C. durissus*.
- cumanensis* Humboldt, 1833. Synonym of *C. d. terrificus*, but see footnote 5 under *C. d. terrificus* in the Check List.
- cyanurus* Rafinesque, 1818. Synonym of *C. h. horridus*.
- decolor* Klauber, 1930. Synonym of *C. v. concolor*.
- dryinas* Linné, 1758. *Nomen indeterminatum*; probably was originally the proper name for the subspecies now known as *C. d. terrificus*.
- durissus* Linné, 1758. Valid species in the genus *Crotalus*.
- edwardsii* Baird and Girard, 1853. Valid subspecies of *S. catenatus*.
- elegans* Schmidt, 1922. Synonym of *C. r. ruber*.
- enyo* Cope, 1861. Valid species in the genus *Crotalus*.
- estebanensis* Klauber, 1949. Valid subspecies of *C. molossus*.
- exalbidus* Boddaert, 1783. Synonym of *C. d. terrificus*.
- exsul* Garman, 1883. Valid species in the genus *Crotalus*.
- fasciatus* Higgins, 1873. Composite synonym of *C. horridus* and others.
- furvus* Lowe and Norris, 1954. Valid subspecies of *C. enyo*.
- giganteus* Brattstrom, 1954. Valid, but extinct, species in the genus *Crotalus*.
- gloydi* Taylor, 1941. Valid subspecies of *C. intermedius*.
- goldmani* Schmidt, 1922. Synonym of *C. m. pyrrhus*.
- gronovii* Laurenti, 1768. *Nomen indeterminatum*; description too brief for recognition.<sup>37</sup>
- hallowelli* Cooper, in Cronise, 1868. *Nomen nudum*. Fixed in the synonymy of *C. v. oreganus* by Van Denburgh, 1922.
- Haploaspis* Cope, 1883. Synonym of *Crotalus*.
- helleri* Meek, 1905. Valid subspecies of *C. viridis*.
- horridus* Linné, 1758. Valid species (type species) in the genus *Crotalus*.
- immaculatus* Latreille, 1802. Synonym of *C. d. terrificus*.
- intermedius* Fischer, 1882. Preoccupied by *intermedius* Troschel, 1865, of which, by pure coincidence, it is also a synonym.
- intermedius* Troschel, in Müller, 1865. Valid species in the genus *Crotalus*.
- jimenezii* Dugès, 1877. Synonym of *C. polystictus*.
- kellyi* Amaral, 1929. Synonym of *C. s. scutulatus*.
- kirtlandi* Holbrook, 1842. Synonym of *S. c. catenatus*.

<sup>37</sup> Cope (in Mitchell, 1860, p. 126) thought this might be *Lachesis mutus*.

- klauberi* Gloyd, 1936. Valid subspecies of *C. lepidus*.  
*lannomi* Tanner, 1966. Valid species in the genus *Crotalus*.  
*laterorepens* Klauber, 1944. Valid subspecies of *C. cerastes*.  
*lautus* Smith, 1946. Synonym of *C. i. intermedius*.  
*lecontei* Hallowell, 1852. Synonym of *C. v. viridis*.  
*lepidus* Kennicott, 1861. Valid species in the genus *Crotalus*.  
*loeflingii* Humboldt, 1833. Synonym of *C. d. terrificus*.  
*lucasensis* Van Denburgh, 1920. Valid subspecies of *C. ruber*.  
*lucifer* Baird and Girard, 1852. Synonym of *C. v. oreganus*.  
*lugubris* Jan, 1859. Synonym of *C. t. triseriatus*.  
*lutosus* Klauber, 1930. Valid subspecies of *C. viridis*.  
*melanurus* Jan, 1859. *Nomen nudum*. Fixed in the synonymy of *C. horridus* by Garman, 1883, and in the synonymy of *C. h. atricaudatus* by Klauber, 1936.  
*meridionalis* Klauber, 1949. Valid subspecies of *C. willardi*.  
*messasaugus* Kirtland, 1838. Synonym of *S. c. catenatus*.  
*mexicana* Jan, 1863. *Nomen nudum*; to be placed in the synonymy *C. h. atricaudatus*.  
*miliarius* Linné, 1766. Valid species (type species) in the genus *Sistrurus*.  
*minor* Catesby, 1743. Pre-Linnean name without standing; represents what is now *S. m. miliarius*.  
*miquihuanus* Gloyd, 1940. Valid subspecies of *C. pricei*.  
*mittellii* Cope, 1861. Valid species in the genus *Crotalus*.  
*molossus* Baird and Girard, 1853. Valid species in the genus *Crotalus*.  
*morulus* Klauber, 1952. Valid subspecies of *C. lepidus*.  
*muertensis* Klauber, 1949. Valid subspecies of *C. mitchellii*.  
*multimaculata* Jan, 1863. Suppressed by the International Commission; synonym of *C. polystictus*.  
*nigrescens* Gloyd, 1936. Valid subspecies of *C. molossus*.  
*nuntius* Klauber, 1935. Valid subspecies of *C. viridis*.  
*oaxacus* Gloyd, 1948. Valid subspecies of *C. basiliscus*.  
*omiltemanus* Günther, 1895. Valid subspecies of *C. intermedius*.  
*oreganus* Holbrook, 1840. Valid subspecies of *C. viridis*.  
*orientalis* Laurenti, 1768. *Nomen indeterminatum*; description too brief for recognition. Probably not a rattlesnake.<sup>28</sup>  
*ornatus* Hallowell, 1854. Synonym of *C. m. molossus*.  
*pallidus* Günther, 1895. Synonym of *C. t. triseriatus*.  
*palmeri* Garman, 1887. Synonym of *C. l. lepidus*.  
*Paracrotalus* Reuss, 1930. Synonym of *Crotalus*.  
*piscivorus* Lacépède, 1789. *Aghistrodon piscivorus*; not a rattlesnake.  
*pleistofloridensis* Brattstrom, 1951. Extinct subspecies of *C. adamanteus*, doubtfully valid.  
*polystictus* Cope, 1865. Valid species in the genus *Crotalus*.  
*potterensis* Brattstrom, 1953. Valid, but extinct, species in the genus *Crotalus*.  
*pricei* Van Denburgh, 1895. Valid species in the genus *Crotalus*.  
*pulverulentus* Cope, 1883. Synonym of *C. v. viridis*.  
*pulvis* Ditmars, 1905. Synonym of *C. unicolor*.  
*pusillus* Klauber, 1952. Valid species in the genus *Crotalus*.  
*pyrrhus* Cope, 1866. Valid subspecies of *C. mitchellii*.  
*ravus* Cope, 1865. Valid species in the genus *Sistrurus*.  
*rhombifer* Latreille, 1802. Synonym of *C. adamanteus*.  
*rhombiferus* Brickell, 1805. Synonym of *C. adamanteus*.  
*ruber* Cope, 1892. Valid species in the genus *Crotalus*.  
*salvini* Günther, 1895. Valid subspecies of *C. scutulatus*.  
*scutulatus* Kennicott, 1861. Valid species in the genus *Crotalus*.  
*semicornutus* Taylor, 1944. Synonym of *C. l. klauberi*.  
*silus* Klauber, 1949. Valid subspecies of *C. willardi*.  
*simus* Latreille, 1802. Synonym of *C. d. durissus*.  
*Sistrurus* Garman, 1883. Valid name of one of the two genera of rattlesnakes. Type species: *S. miliarius*. *Sistrurus* is considered a subgenus under *Crotalus* by Brattstrom, 1964a, p. 250, a classification in which I do not concur.

<sup>28</sup> Considered a synonym of *dryinas* (= *terrificus*) by Desmarest, Hist. Nat. Lacépède, vol. 1, p. 423, 1814.

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*sonoraensis* Kennicott, 1861. Synonym of *C. atrox*.  
*stejnegeri* Dunn, 1919. Valid species in the genus *Crotalus*.  
*stephensi* Klauber, 1930. Valid subspecies of *C. mitchellii*.  
*streckeri* Gloyd, 1935. Valid subspecies of *S. miliarius*.  
*strepitans* Daudin, 1803. Synonym of *C. d. terrificus*.  
*tergeminus* Say, 1823. Valid subspecies of *S. catenatus*.  
*terrificus* Laurenti, 1768. Valid subspecies of *C. durissus*.  
*tesselatus* Hermann, 1804. *Nomen indeterminatum*; description too brief for recognition.  
*tigris* Kennicott, 1859. Valid species in the genus *Crotalus*.  
*tortugensis* Van Denburgh and Slevin, 1921. Valid species in the genus *Crotalus*.  
*totonacus* Gloyd and Kauffeld, 1940. Valid subspecies of *C. durissus*.  
*transversus* Taylor, 1944. Valid species in the genus *Crotalus*.  
*triseriatus* Wagler, 1830. Valid species in the genus *Crotalus*.  
*tzabcan* Klauber, 1952. Valid species in the genus *Crotalus*.  
*unicolor* Van Lidth de Jeude, 1887. Valid species in the genus *Crotalus*.  
*Urocrotalon* Fitzinger, 1843. Synonym of *Crotalus*.  
*Uropsophus* Wagler, 1830. Synonym of *Crotalus*.  
*vegrandis* Klauber, 1941. Valid subspecies of *C. durissus*.  
*viridis* Rafinesque, 1818. Valid species in the genus *Crotalus*.  
*willardi* Meek, 1905. Valid species in the genus *Crotalus*.  
*zetazomae* Brickell, 1805. Synonym of *C. h. atricaudatus*.

CROSS-INDEX: VERNACULAR (OR COMMON) TO  
TECHNICAL NAMES

(The word “rattlesnake” is omitted from the titles. Where a collective word, such as “diamond” or “speckled,” applies to several subspecies, all are listed.)

Angel de la Guarda Island speckled	<i>C. mitchellii angelensis</i>
Arizona black	<i>C. viridis cerberus</i>
Arizona ridge-nosed	<i>C. willardi willardi</i>
Aruba Island	<i>C. unicolor</i>
Autlán	<i>C. lannomi</i>
Banded rock	<i>C. lepidus klauberi</i>
Black-tailed	<i>C. molossus</i> subspecies
Canebrake	<i>C. horridus atricaudatus</i>
Carolina pigmy	<i>S. miliarius miliarius</i>
Cedros Island diamond	<i>C. exsul</i>
Central American	<i>C. durissus durissus</i>
Central-plateau dusky	<i>C. triseriatus triseriatus</i>
Cerralvo Island	<i>C. enyo cerralvensis</i>
Colorado Desert sidewinder	<i>C. cerastes laterorepens</i>
Coronado Island	<i>C. viridis caliginis</i>
Cross-banded mountain	<i>C. transversus</i>
Del Nido ridge-nosed	<i>C. willardi amabilis</i>
Desert massasauga	<i>S. catenatus edwardsii</i>
Diamond or diamondback	<i>C. adamanteus</i> , <i>C. atrox</i> , <i>C. ruber</i> , etc.
Dusky	<i>C. triseriatus</i> subspecies and <i>C. pusillus</i>
Dusky pigmy	<i>S. m. barbouri</i>
Eastern diamondback	<i>C. adamanteus</i>
Eastern massasauga	<i>S. catenatus catenatus</i>
Eastern twin-spotted	<i>C. pricei miquihuanus</i>

El Muerto Island speckled	<i>C. m. muertensis</i>
Grand Canyon	<i>C. viridis abyssus</i>
Great Basin	<i>C. viridis lutosus</i>
Hopi	<i>C. viridis nuntius</i>
Huamantlan	<i>C. scutulatus salvini</i>
Lance-headed	<i>C. polystictus</i>
Long-tailed	<i>C. stejnegeri</i>
Lower California	<i>C. enyo</i>
Massasauga	<i>S. catenatus</i> subspecies
Mexican black-tailed	<i>C. molossus nigrescens</i>
Mexican lance-headed	<i>C. polystictus</i>
Mexican pigmy	<i>S. rarus</i>
Mexican west-coast	<i>C. basiliscus basiliscus</i>
Midget faded	<i>C. viridis concolor</i>
Mojave	<i>C. scutulatus scutulatus</i>
Mojave Desert sidewinder	<i>C. cerastes cerastes</i>
Mottled rock	<i>C. lepidus lepidus</i>
Neotropical	<i>C. durissus</i> subspecies
Northern black-tailed	<i>C. molossus molossus</i>
Northern Pacific	<i>C. viridis oreganus</i>
Northwestern Neotropical	<i>C. durissus culminatus</i>
Oaxacan	<i>C. basiliscus oaxacus</i>
Oaxacan small-headed	<i>C. intermedius gloydi</i>
Omitteman small-headed	<i>C. intermedius omittemanus</i>
Pacific	<i>C. v. oreganus</i> or <i>C. v. helleri</i>
Panamint	<i>C. mitchellii stephensi</i>
Pigmy	<i>S. miliarius</i> subspecies and <i>S. rarus</i>
Prairie	<i>C. viridis viridis</i>
Queretaran dusky	<i>C. triseriatus aquilus</i>
Rattleless	<i>C. catalinensis</i>
Red diamond	<i>C. ruber ruber</i>
Ridge-nosed	<i>C. willardi</i> subspecies
Rock	<i>C. lepidus</i> subspecies
Rosario	<i>C. enyo furvus</i>
San Esteban Island	<i>C. molossus estebanensis</i>
San Lucan diamond	<i>C. ruber lucasensis</i>
San Lucan speckled	<i>C. mitchellii mitchellii</i>
Santa Catalina Island	<i>C. catalinensis</i>
Sidewinder	<i>C. cerastes</i> subspecies
Small-headed	<i>C. intermedius</i> subspecies
Sonoran Desert sidewinder	<i>C. cerastes cercobombus</i>
South American	<i>C. durissus terrificus</i> (See footnote 7, p. 35.)
Southern Pacific	<i>C. viridis helleri</i>
Southern ridge-nosed	<i>C. willardi meridionalis</i>
Southwestern speckled	<i>C. mitchellii pyrrhus</i>
Speckled	<i>C. mitchellii</i> subspecies
Tamaulipan rock	<i>C. lepidus morulus</i>
Tancitaran dusky	<i>C. pusillus</i>
Tiger	<i>C. tigris</i>
Timber	<i>C. horridus horridus</i>
Tortuga Island diamond	<i>C. tortugensis</i>
Totalcan small-headed	<i>C. intermedius intermedius</i>
Totonacan	<i>C. durissus totonacus</i>
Twin-spotted	<i>C. pricei</i> subspecies
Uracoan	<i>C. vegrandis</i>

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West Chihuahua ridge-nosed	<i>C. willardi silus</i>
Western	<i>C. viridis</i> subspecies
Western diamondback	<i>C. atrox</i>
Western massasauga	<i>S. catenatus tergeminus</i>
Western pigmy	<i>S. miliarius streckeri</i>
Western twin-spotted	<i>C. pricei pricei</i>
Yucatan Neotropical	<i>C. durissus tzabcan</i>

## KEYS TO THE RATTLESNAKES

When a taxonomist engages in the classification of a group of snakes such as the rattlesnakes, he brings to bear whatever knowledge he may have concerning the characteristics of the individuals that compose the group. He endeavors to discover subgroup differences, whereby the individuals may be allocated into separate categories, particularly into species and subspecies. Not only does he endeavor to divide the available animals into these smaller (more restricted) categories, to which separate names are assigned for purposes of recognition (taxonomy), but also he attempts to determine group relationships, both present and historical (phylogeny).

In making taxonomic and phylogenetic studies of this type, the worker accumulates a considerable fund of data involving various kinds of characters. The usefulness of the characters in classification depends on their within-group consistency and between-group divergence. No single character-category is universally successful in attaining this segregative purpose. One character may permit segregating group A from B, but fail to separate B from C; yet a second character may show that B does differ from C. Some characters may be readily ascertained in every specimen; others, skeletal characters for example, may be studied in only a few. Certain characters, especially those involving body proportions (e.g., the ratio of head to body length) change during the lifetime of every individual, which must not be forgotten when comparisons are to be made.

Some of the characters that are used in the classification of rattlesnakes—and most of them in the classification of other snakes, as well—are these: form, color, and pattern; scale numbers, arrangements, and contacts (squamation); body-part proportions; osteology; rattle dimensions; male organs; venom quality; and blood characteristics. Some of these characters—the best example is squamation—can, with a little practice, be evaluated readily for each specimen. Others involve highly technical processes, as, for example, the study of blood constituents (Deutsch and McShan, 1949, p. 219; Cohen, 1951, p. 6; 1954, p. 98; 1955, p. 394; and Des-sauer and his associates, 1956, 1957, 1958, and 1962).

Elsewhere in this book I have discussed, and have often tabulated, the differences in characters that distinguish the many subspecies of rattlesnakes. But the reader would have a difficult time searching through these compilations in an endeavor to identify some particular specimen. To expedite such a project, identification keys are provided; this is a customary practice in all branches of biology. In these keys, instead of presenting a mass of indigestible data on each subspecies, only the most easily ascertainable character or characters that will segregate one subspecies from another are used. Further, the decisions on these differences are arranged in a particular order that will permit the shortest path to an accurate conclusion.

My purpose in dividing what might have been a single all-inclusive key into six geographically separate keys has been to secure simplicity and accuracy of use at the expense of some duplication. It is true of the rattlesnakes, as it is of many animals, that subspecies widely separated geographically are sometimes much alike superficially. By restricting these keys geographically, I have been able to shorten and definitize the character alternatives. It will indeed be rare

that anyone will wish to identify a specimen whose origin will not be known, at least to the extent of confining it to one of these six major geographical subdivisions: Canada; United States east of the Mississippi River; United States west of the Mississippi River; Mexico, exclusive of Baja California; Baja California and adjacent islands; Central and South America. Once the user has selected the right geographical key, he will reach an identification more quickly and accurately than would be possible were dependence placed on a single all-inclusive key. Where a subspecies occurs in two or more geographical areas, it will be found included in each key; and even when its presence in an area is somewhat questionable, it is included, so that a correct determination will result if the known range should be extended into the doubtful area by new discoveries.

The keys are of the so-called dichotomous type, in which the user proceeds by the selection of one course from each of successive pairs of alternatives. Take the key to the rattlesnakes of Mexico as an example. Start at 1 and decide whether the specimen to be identified is correctly described by paragraph 1*a* or 1*b*. If the former is true, the snake belongs to the genus *Sistrurus*; if the latter, to the genus *Crotalus*. Assume, in this example, that it is *Crotalus*. Note that the figure 3 appears at the end of the final line in paragraph 1*b*; this is an instruction to proceed to the paragraphs headed 3*a* and 3*b*. Now decide which of these alternative descriptions fits the specimen in hand. If it fits description 3*a*, then the snake is *Crotalus cerastes*, and it is necessary to proceed to 4*a* and 4*b* to find whether it belongs to the subspecies *cercobombus* or *laterorepens*. If, on the other hand, 3*b* properly describes the specimen, then you are directed by the figure 5 at the end of the line to proceed to 5*a* and 5*b* for the next choice, and so on. Thus, by successive selections of one of the pairs of alternatives, a final decision is eventually reached.

When an identification has been made, the conclusion should be checked against the geographical tables (tables 2:1 to 2:6) or range maps (figs. 2:1 to 2:10) to see whether the subspecies arrived at does occur where the specimen was found. The specimen photographs (figs. 2:11 to 2:82) and scale-character table (table 2:7) will also be found useful. Thus an inaccurate conclusion may be avoided, even if some peculiarity of the specimen or ambiguity in the keys has caused a wrong turning at one of the branch points. If the locality where a specimen was captured is known with accuracy, always doubt the key or its method of use before taking it for granted that some subspecies has been found in an area far from its previously known range.

In using a key of this type, it is always essential to begin at 1*a*, otherwise an accurate identification may not be reached.

Sometimes it will be found, when each of the alternatives lists several character differences, that the specimen in hand indicates that one course should be followed if the decision is based on one character, but that the alternative course should be taken based on another. Then the user should be guided first by geographical considerations, especially if one course should indicate the presence of a particular subspecies in an area distant from its known range. Second, the user should be guided by the relative importance and stability of the several characters cited at this particular branch point in the key, a requirement necessitating some experience in the genus.

The differentiation between the subspecies of a single species is seldom as consistent and clear-cut as the distinction between species. Even where the subspecies are well differentiated, as they occur at their respective centers of population, their differential characters are no longer sharply distinctive in areas where their ranges approach each other. Such areas of intergradation are likely to be broad, with subspecies poorly differentiated, where ecological changes are also broad and gradual. Examples of such areas where the allocation of specimens to particular subspecies by the use of the keys is difficult, are, first, the place where the subspecies *Crotalus viridis viridis*, *C. v. concolor*, and *C. v. nuntius* approach each other in the vicinity of Four Corners (the point where the states of Utah, Colorado, New Mexico, and Arizona meet) ; and, second, in the Texas Panhandle and southeastern Colorado, where the two subspecies of *Sistrurus catenatus*, that is *S. c. tergeminus* and *S. c. edwardsii*, intermingle.<sup>30</sup>

<sup>30</sup> Maslin, 1965, p. 31, shows the difficulty in determining to which subspecies, *S. c. edwardsii* or *S. c. tergeminus*, the massasaugas of Colorado, belong.

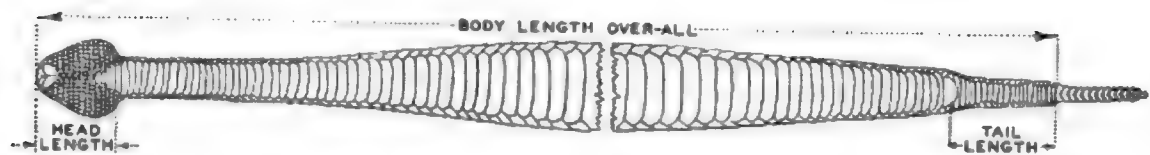


Fig. 2:83. Methods of measurement.

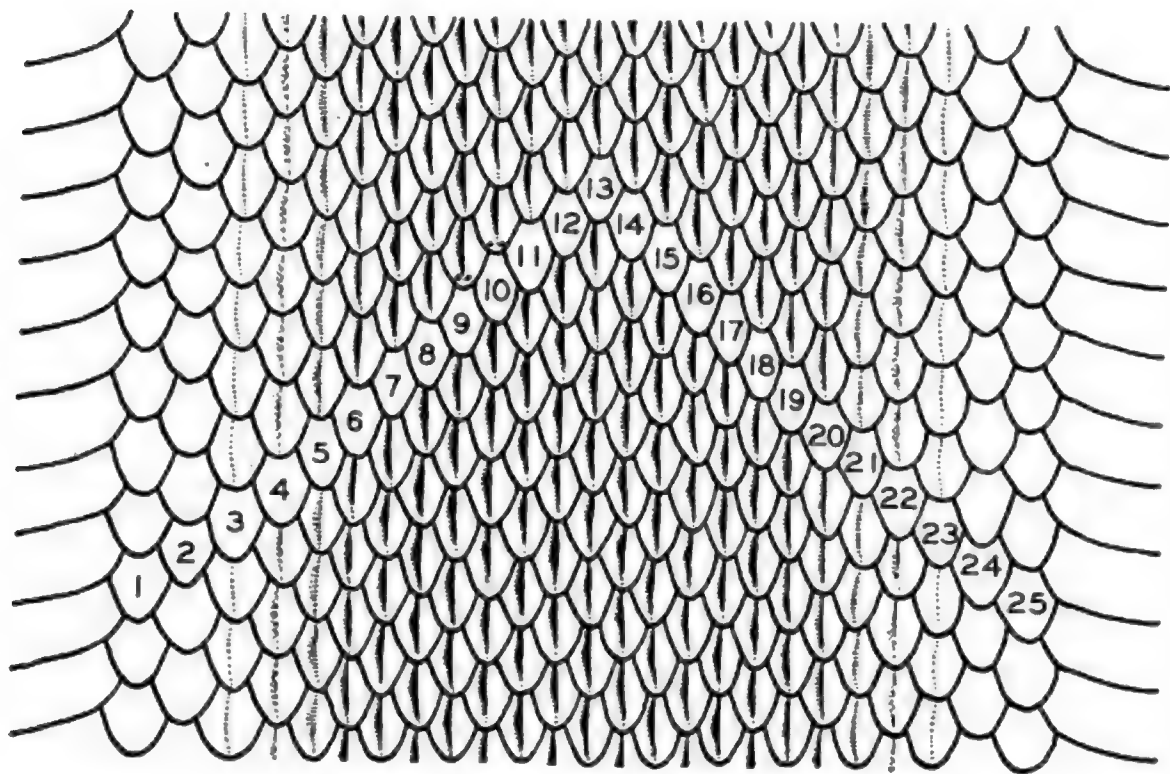


Fig. 2:84. Method of counting dorsal scale rows.

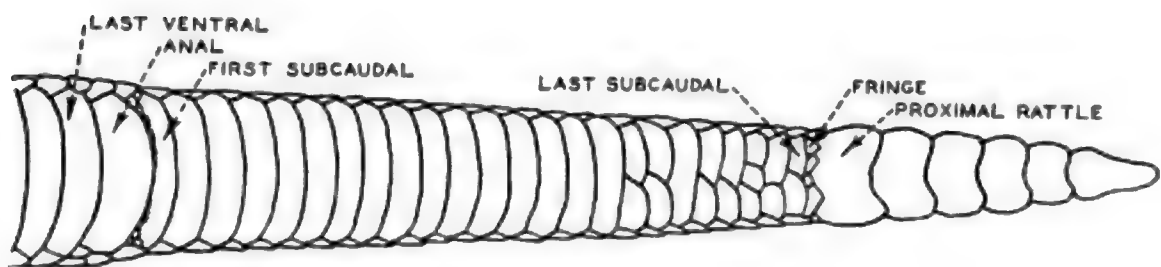


Fig. 2:85. Ventral view of tail with nomenclature.

In addition to the six geographical keys to the rattlesnakes that I have prepared, I also present three keys prepared by Bayard H. Brattstrom at the University of California, Los Angeles, as a part of his study of the crotalids (1964a, p. 187). These keys include the following:

- Key to the genera of the Crotalidae based on external characters
- Key to the genera of the Crotalidae based on the adult skull
- Key to the species of the genera *Crotalus* and *Sistrurus* based on the adult skull

## GLOSSARY

This glossary is intended to explain the various terms, particularly those of squamation (scalation), in the keys that follow.

- Anal plate.** The large plate covering the vent (fig. 2:85). It marks the division between body and tail.
- Angle of the mouth.** The point at which the upper and lower jaws diverge (fig. 2:90). Also called the rictus of the mouth or the commissure. It lies between the last supralabial and last infra-labial (fig. 2:88).
- Apical scale pits.** A pair of depressions faintly evident on the posterior end of each scale; usually most evident dorsally near the tail or on the tail. They are shown, rather exaggerated, in the scales immediately above scales numbers 9 and 10, figure 2:84.
- Body blotches.** The blotches of the primary dorsal series, which are counted from the posterior edge of the head to a point opposite the anus; the tail rings are not included. On the sides there are usually additional series of smaller blotches known as the lateral, auxiliary, or secondary blotches, often in several rows, one below the other. In many species of rattlesnakes, especially on the posterior half or third of the body, the main dorsal blotches merge with the laterals to form crossbars, chevrons, or rings (fig. 2:127).
- Button.** See *Rattles*.
- Canthals.** The border scales of the crown between the internasals and the supraoculars (figs. 2:87 and 2:88). They are sometimes paired and in contact, in which case they are synonymous with prefrontals (fig. 2:125).
- Canthus rostralis.** The outer edge of the flat area of the crown, where it turns downward on the side, extending from the rostral to the supraocular (fig. 2:87).
- Caudals.** See *Subcaudals*.
- Commissure.** See *Angle of the mouth*.
- Complete.** An unbroken rattle string with the button intact.
- Confluent.** Joined together.
- Crown.** The forward part of the top of the head, that is, the area in *Crotalus* occupied by the 9 large plates in *Sistrurus* (figs. 2:86 and 2:87).
- Distal.** Distant from the point of attachment; the opposite of proximal.
- Dorsal scales.** See *Scale rows*.
- Foveals.** Small scales surrounding the pit exteriorly that have no other regular designations. (See also *Lacunals*.) The prefoveals usually fall within the triangle between the lacunals, loreal, postnasal, and supralabials (fig. 2:91). They sometimes extend forward to the rostral between the prenasal and the first supralabial (fig. 2:121 and 2:148). The subfoveals lie between the lacunals and the supralabials. If a lacunal contacts a supralabial, thus interrupting a complete row of subfoveals, then all foveals are considered to be prefoveals and postfoveals, rather than subfoveals. Postfoveals may be assumed to terminate at the interoculabials.
- Fringes.** See *Rattle-fringe scales*.
- Frontal.** The large plate between the supraoculars in *Sistrurus* (fig. 2:86). In *Crotalus* this space is filled with scales more or less irregularly disposed (fig. 2:87), and is referred to as the frontal area, and the scales as the intersupraoculars. When the "minimum scales between the supraoculars" are specified, the path traversing the fewest scales is meant; this is usually at the anterior part of the frontal area as in figures 2:125 and 2:130.

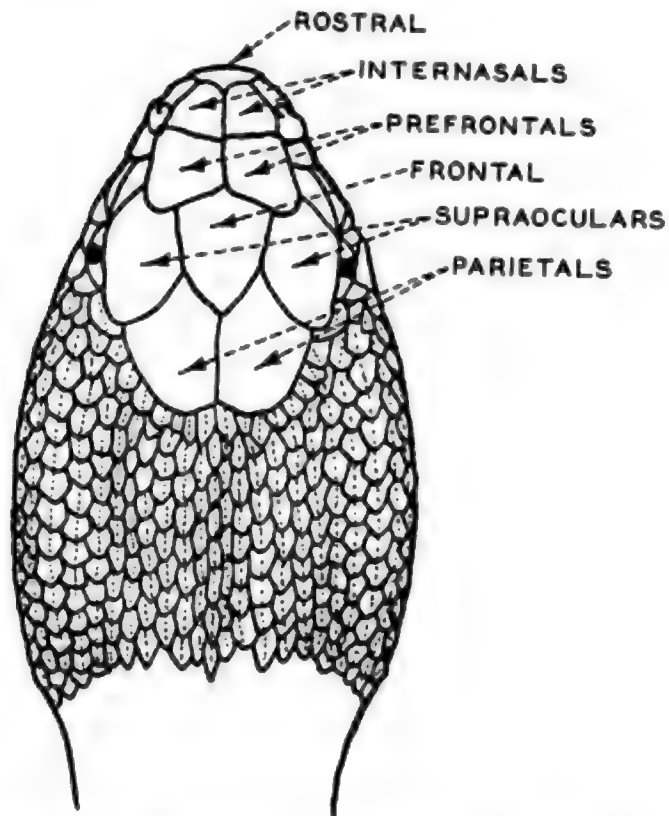


Fig. 2:86. Nomenclature of head scales of *Sistrurus*.

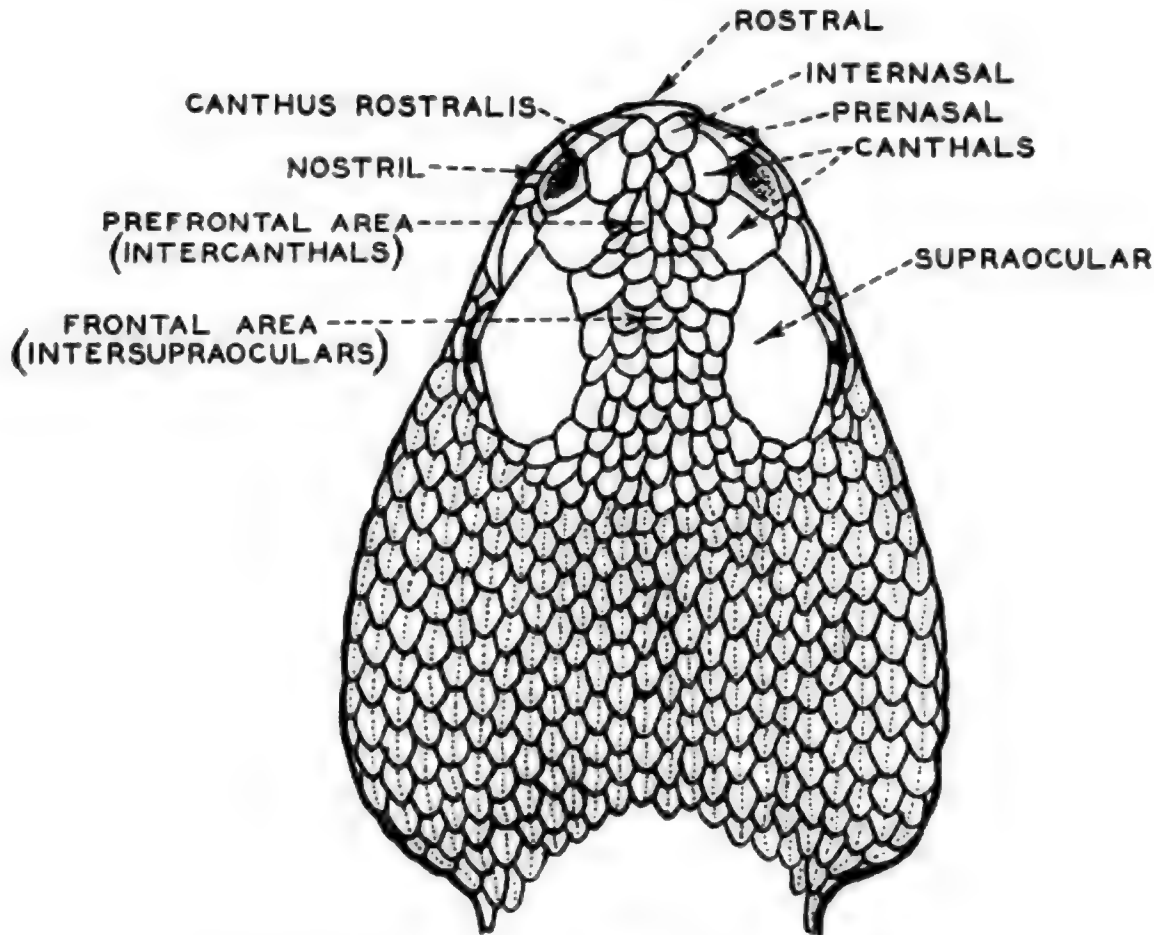


Fig. 2:87. Nomenclature of head scales of *Crotalus*, dorsal view.

**Frontal area.** See *Frontal*.

**Genials.** The genials, or chin shields, are a pair of enlarged scales back of the first infralabials (figs. 2:89 and 2:90). Occasionally the posterior tips of the first infralabials are cut off to form an extra pair of triangular scales, which are called intergenials (fig. 2:145). Snakes other than rattlesnakes often have two pairs of genials: an anterior and posterior.

**Granules.** Tiny scales.

**Ground color.** The basic or background color between blotches or rings, shown in medium gray in figures 2:101, 2:120, and 2:128.

**Gulars.** The small scales covering the underside of the head, between the infralabials on the opposite sides of the head, and not otherwise specifically named (fig. 2:90).

**Head length.** See *Lengths*.

**Head marks.** Although there is a considerable variation in the head marks of the rattlesnakes, there are some that occur in many species; these are indicated as to general position and direction in figures 2:92 and 2:93. The light supraocular crossbars in some species are present only on the supraoculars and not in the intervening frontal area. Nearly all species have a dark streak extending from the eye toward the angle of the mouth.

**Infralabials.** See *Labials*.

**Infraloreals.** See *Loreals*.

**Intercanthals.** Scales in the prefrontal area between the canthals (fig. 2:87).

**Internasals.** The scales in contact with the rostral from nasal to nasal regardless of size (figs. 2:86 and 2:87). In most rattlesnakes there are two (fig. 2:117); in *viridis* and its subspecies, generally three or more (fig. 2:116).

**Interoculabials.** Scales between the eye and the lip, including a subocular and a supralabial at the upper and lower ends of the series. They are usually counted below the center of the eye (fig. 2:91).

**Interpreoculars.** Small scales occasionally interposed between the large upper preocular and the crescentic lower preocular (fig. 2:91).

**Interspace.** The space between blotches, chevrons, or rings.

**Intersupraoculars.** See *Frontal*.

**Labials.** Bordering the mouth above are the supralabials, or upper labials (figs. 2:88 and 2:89), which extend from the rostral to the angle of the mouth (also called the rictus of the mouth, or commissure). The rostral is not counted as one of the supralabials. Similarly the infralabials, or lower labials, extend along the lower lip from the mental to the angle of the mouth (figs. 2:88, 2:89, and 2:90). The first infralabials are sometimes divided transversely (fig. 2:132). When counting infralabials, the mental is not included.

**Lacunals.** Scales lining the pit interiorly (fig. 2:91). They usually are visible exteriorly; if they are entirely exterior, they are to be considered foveals rather than lacunals.

**Lengths.** The over-all length is measured from the tip of the snout (rostral) to the forward edge of the proximal rattle (fig. 2:83). Head length is measured from the rostral to a line joining the posterior tips of the mandibular bones. Tail length is from the center of the anal plate to the forward edge of the proximal rattle.

**Lobe.** One of the several parts (usually 3 in adults) between the constrictions of a single rattle segment. The anterior lobe of every rattle is always visible; the posterior lobes of any but the distal rattle are always hidden by the rattle that follows it behind (figs. 2:94 and 2:95).

**Loreals.** The scales (one or more) on the side of the head between the postnasal and the preoculars (fig. 2:88). No species of rattlesnake is regularly without at least one loreal on each side, although rarely an individual may have none. Often there are two loreals: an upper or supra-loreal, and a lower or infraloreal.

**Matrix.** The fleshy terminus of the tail upon which each successive rattle is formed. It is faintly visible through the semitransparent proximal rattle lobe.

**Mental.** The triangular scale at the anterior tip of the lower jaw (figs. 2:89 and 2:90). Occasionally the posterior tip of the mental may be cut off to form a submental (fig. 2:146).

**Nasals.** A pair of scales on either side of the nostril, called respectively, the prenasal and postnasal (figs. 2:88 and 2:89).<sup>40</sup> In some species (e.g., *lepidus*) the prenasals and postnasals may be joined together above the nostril.

<sup>40</sup> H. M. Smith (1946, p. 82) prefers the terms "preseminasal" and "postseminasal."

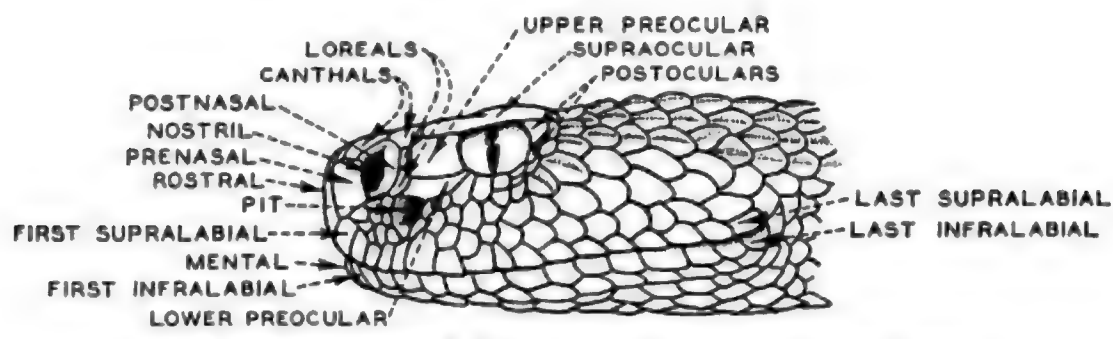


Fig. 2:88. Nomenclature of head scales of *Crotalus*, lateral view.

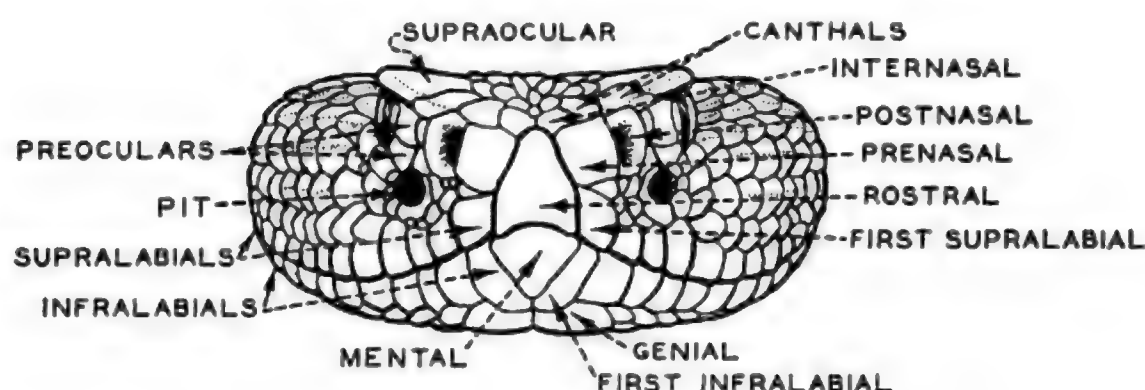


Fig. 2:89. Nomenclature of head scales of *Crotalus*, front view.

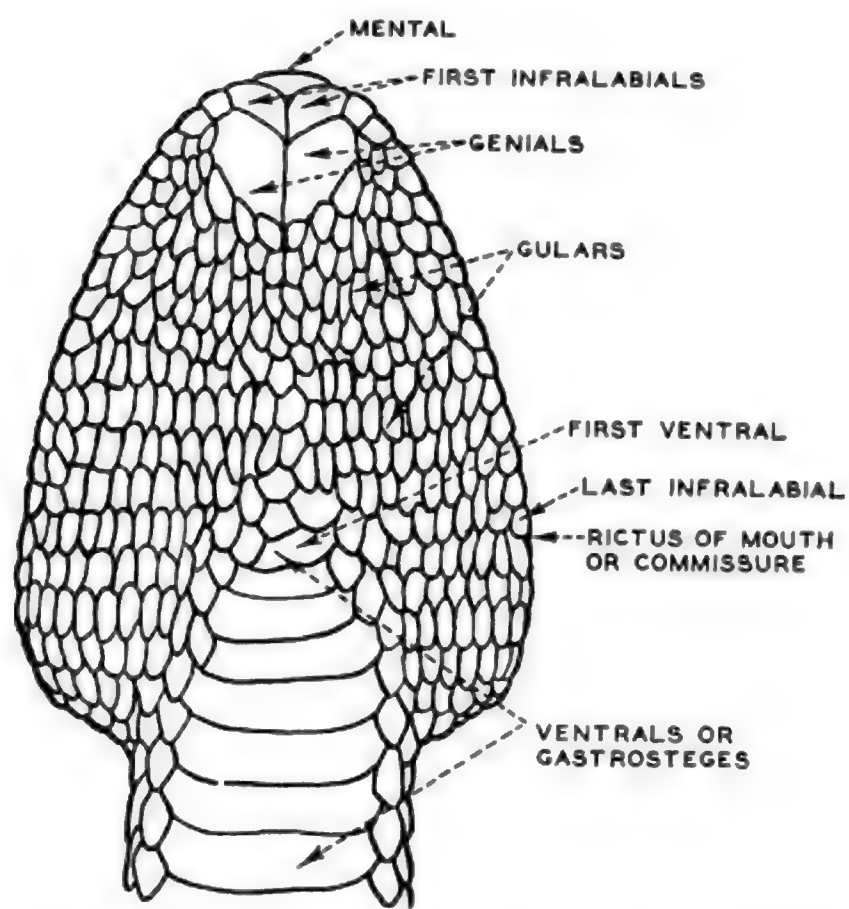


Fig. 2:90. Nomenclature of head scales of *Crotalus*, ventral view.

**Occipital area.** The posterior top of the head back of the parietal area—that is, back of the parietal plates in figure 2:86.

**Oculars.** The scales surrounding the eye. The supraoculars are large and jut over the eyes (fig. 2:88). In front of the eyes there are usually two preoculars: the upper larger, the lower narrow and crescent-shaped. It is usually difficult to determine which scale should be considered the lowest postocular, and which the last subocular.

**Orbit.** The eye opening.

**Paravertebral.** On each side of the middorsal line.

**Parietal area.** The area of the top of the head occupied by the parietal plates in *Sistrurus* (fig. 2:86).

**Parietals.** A pair of large plates posterior to the supraoculars and frontal in *Sistrurus* (fig. 2:86).

This area is occupied by irregular scales in *Crotalus* (fig. 2:87).

**Pit.** A deep depression on the side of the head below and back of the nostril (figs. 2:88 and 2:89).

It is the external opening of a sensory organ.

**Pit scales.** See *Lacunals* and *Foveals*.

**Plate.** Any large, flat scale, particularly on the head or belly.

**Postfoveals.** See *Foveals*.

**Postloreal.** Small scales posterior to the upper loreal and above the upper preocular (fig. 2:91); they cannot always be differentiated from postsupraloreals.

**Postnasals.** See *Nasals*.

**Postoculars.** See *Oculars*.

**Postrostral.** A small scale bounded by the rostral, prenasal, and first supralabial (fig. 2:140). If there is an unbroken line of foveals to the rostral (as in fig. 2:121), the postrostral is counted as a foveal.

**Postsupraloreals.** One or more small scales posterior to the loreal or upper loreal, and below the canthals (fig. 2:91). See also *Postloreal*.

**Prebutton.** See *Rattles*.

**Preciliaries.** Small scales above the regular upper preocular, in contact with the eye and the supraocular (fig. 2:91).

**Prefoveals.** See *Foveals*.

**Prefrontals.** In *Sistrurus* the two large plates posterior to the internasals (fig. 2:86). In *Crotalus*, with a few exceptions—of which *pusillus*, some *durissus*, and some *molossus* are examples (fig. 2:125)—this space (often referred to as the prefrontal area) is filled with irregularly disposed scales called the intercanthals (fig. 2:87).

**Prenasals.** See *Nasals*.

**Preoculars.** See *Oculars*.

**Presupraloreals.** One or more small scales anterior to the loreal or upper loreal and below the canthals (fig. 2:91).

**Process.** A projecting part or extension.

**Proximal.** Toward the point of attachment; the opposite of distal.

**Punctations.** Small spots or dots.

**Rattle-fringe scales.** The last scales on the tail that cover the forward edge of the rattle (fig. 2:85).

**Rattles.** The rattle terminology is illustrated in figures 2:94 and 2:95. The proximal rattle is that next to the tail and is the one most recently added to the string. The button (or rattle-button) is the first permanent rattle acquired by a young snake, the rattle present at birth (the prebutton—fig. 5:3) being invariably lost with the first shedding of the skin. The button remains as the posterior terminus of the rattle-string until lost by breakage<sup>41</sup>; it is usually present in juveniles or young adults, but rarely in older specimens. The rattle width (also called the dorsoventral width) of any segment is measured as indicated in figure 2:95. In these keys the widths of the proximal rattle and of the button are occasionally used.

**Rostral.** The large scale on the front of the nose (figs. 2:86, 2:87, 2:88, and 2:89).

**Scale-boss.** A knobby prominence, tuberculation, or swelling on the posterior part of each scale, especially evident on the middorsal rows of some species, particularly *durissus*. It is to a certain extent independent of the keeling (or central ridge on each scale) that is present in all rattlesnake species on all but the one or two lowest dorsolateral rows.

**Scale rows.** Where the number of dorsal scale rows is given, the number at mid-body is meant, beginning with the row next to the ventrals on one side and ending with the corresponding

<sup>41</sup> Except in *C. catalinensis*.

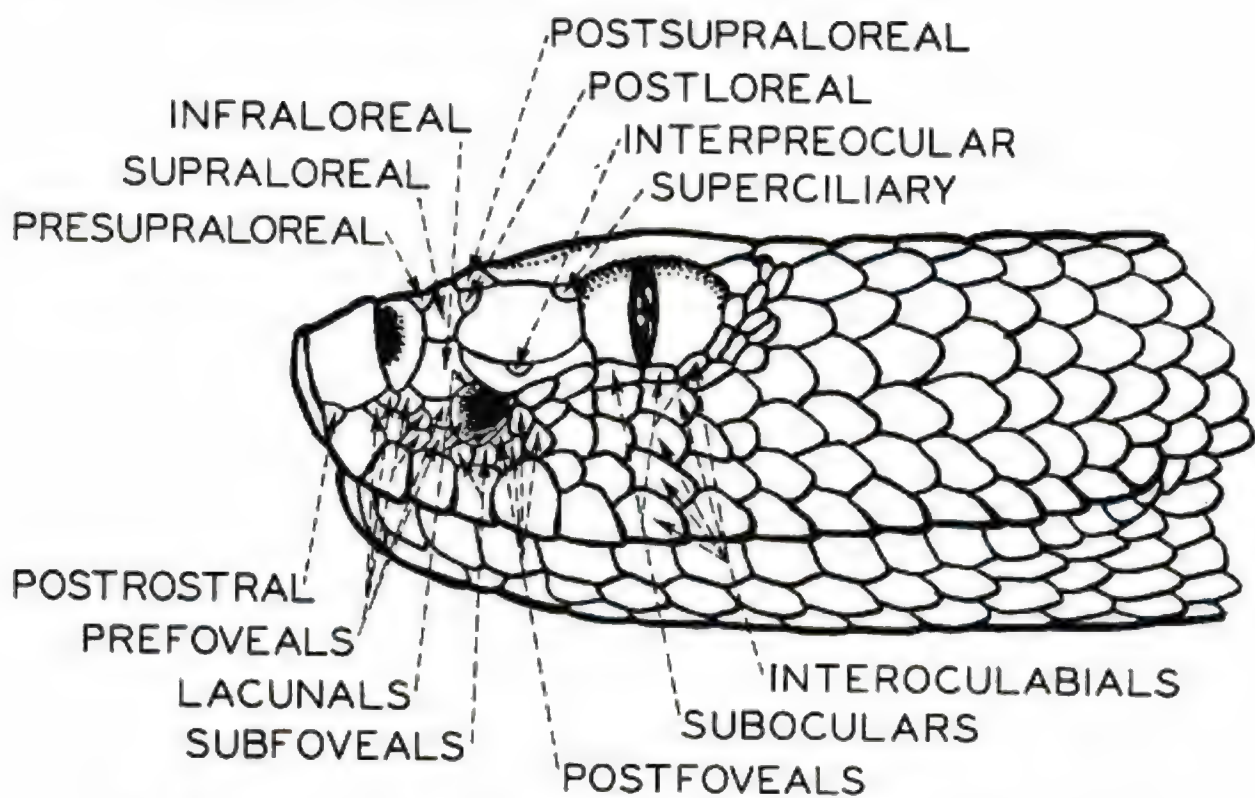


Fig. 2:91. Nomenclature of head scales of *Crotalus*, lateral view, showing some scales not designated in fig. 2:88, together with others of less frequent occurrence.

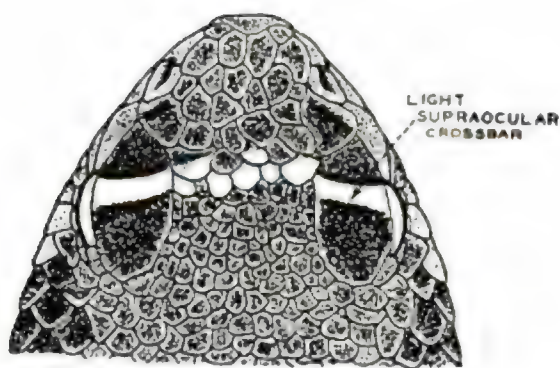


Fig. 2:92. Head pattern of *Crotalus*, dorsal view.

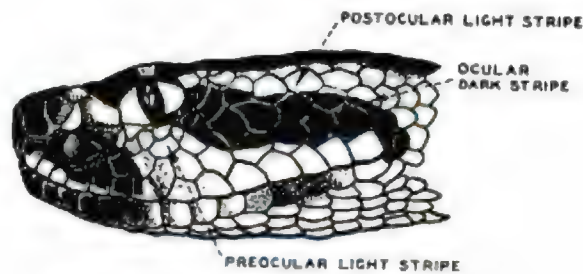


Fig. 2:93. Head pattern of *Crotalus*, lateral view.

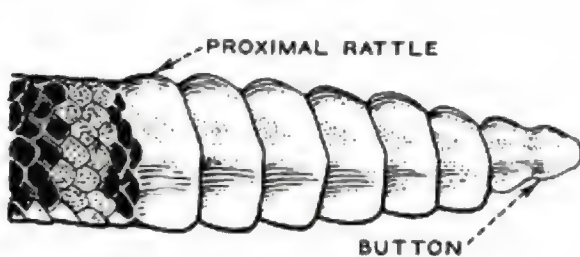


Fig. 2:94. Complete rattle with button.

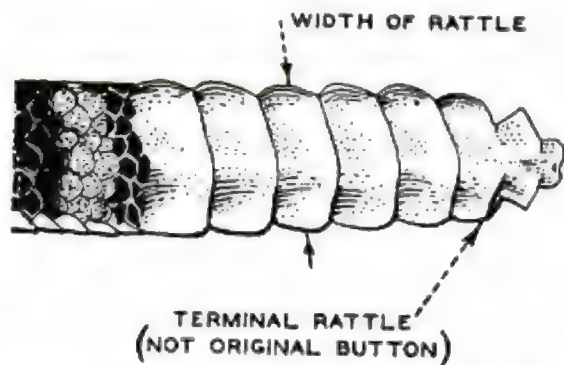


Fig. 2:95. Incomplete rattle; also showing how rattle width is measured.

- row on the other (fig. 2:84). Occasionally the scale rows at the center of the tail are referred to; these should be counted midway between the anal plate and the anterior edge of the proximal rattle.
- Scales long or scales wide.* To draw comparisons between the sizes of blotches, their lengths and widths are often expressed in terms of the number of scales or scale rows encompassed. Scales long means the number of scales within a blotch, end to end lengthwise of the body of the snake. Scales wide means the number of scale rows (counted as in fig. 2:84) encompassed within a blotch across the body.
- Scute.* A large flat scale; a term often applied to the ventrals.
- Skull.* For the names of the bones of the skull see figures 11:1 to 11:4.
- Stippled.* Marked with dots.
- Sub-*. This prefix applied to a scale usually means below or under. A subloreal is below the main loreal. Applied to a geometrical adjective, such as circular, quadrate, or hexagonal, it signifies likeness. That is, subelliptical means somewhat or nearly elliptical, but not precisely so.
- Subcaudals.* The subcaudals (caudals or urosteges) are counted beginning with the first scale on the mid-ventral line posterior to the anal plate and ending with the last scale anterior to the proximal rattle (fig. 2:85). Divided scales—that is, those having mid-ventral sutures, frequently found toward the beginning or end of the series—are counted as if undivided. The fringe of small and irregular scales that usually covers the anterior edge of the rattle is not counted as a caudal.
- Subfoveals.* See *Foveals*.
- Suboculars.* Scales below and touching the eye (fig. 2:88).
- Supralabials.* See *Labials*.
- Supraloreals.* See *Loreals*.
- Supraoculars.* The large plates above each eye (fig. 2:86, 2:87, 2:88, and 2:89). See also *Oculars*.
- Suture.* A division or deep crease between two scales or plates, or the parts of a plate.
- Tail length.* See *Lengths*.
- Tail rings.* The dorsal rings between the anus and the proximal rattle (fig. 2:126). In some species they are obscure and can be counted only approximately if at all.
- Tuberculate.* See *Scale-boss*.
- Ventrals.* The large plates on the belly. The ventral plates (sometimes called the gastrosteges) are counted by beginning with the first scale on the underside of the head that is distinctly wider than long (fig. 2:90), and ending with the scale anterior to the anal plate, but not including the latter (fig. 2:85).
- Vertebra.* For the designations of the parts of a vertebra see figures 3:1–3:3.
- Vertebral process.* A ridge along the center of the back accentuated in some species, of which *durissus* is the best example.

KEY TO THE RATTLESNAKES OF CANADA

- 1a. Top of head with large plates anteriorly, usually 9 in number (fig. 2:96)  
*Sistrurus catenatus catenatus* (fig. 2:76)
- 1b. Top of head with small scales anteriorly (fig. 2:97) ..... Genus *Crotalus* 2
- 2a. Two internasals (fig. 2:117); dark rings on the tail not well differentiated from the ground color; tail often black.....*Crotalus horridus horridus* (fig. 2:30)
- 2b. Usually more than two internasals (scales between nasals and in contact with rostral, regardless of size or position, fig. 2:116); dark tail rings clearly contrasting with a lighter background ..... 3<sup>42</sup>
- 3a. Anterior dark tail rings usually olive to brown, on a buff, greenish, or olive background; rings narrower, usually 2 scales wide laterally.....*Crotalus viridis viridis* (fig. 2:62)
- 3b. Anterior dark tail rings usually dark-brown to black, on a light-gray background; rings wider, usually 3 scales wide laterally.....*Crotalus viridis oregonus* (figs. 2:70 and 2:71)

<sup>42</sup> When this point in the key has been reached, the final decision can, if desired, be made entirely on geographical considerations. In Canada, *C. v. viridis* occurs only in Saskatchewan and Alberta; *C. v. oregonus* only in British Columbia. No other kinds of rattlesnakes are found in these provinces.

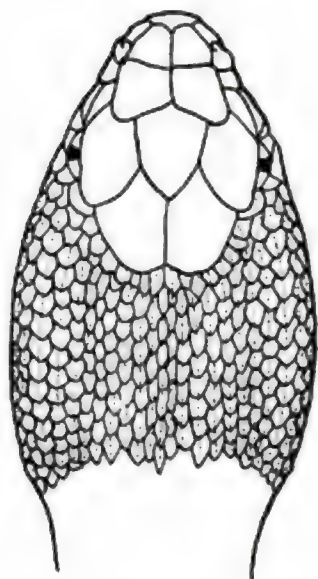


Fig. 2:96. Dorsal head plates of *Sistrurus* (*S. catenatus*).

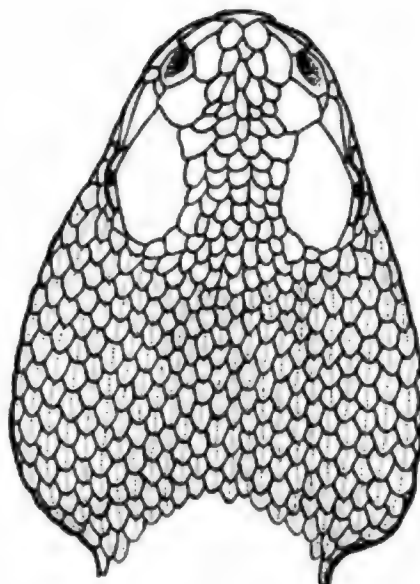


Fig. 2:97. Dorsal head scales of *Crotalus* (*C. atrox*).

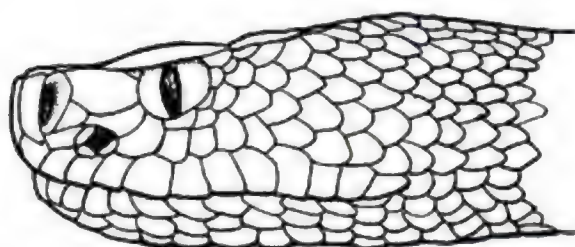


Fig. 2:98. *S. catenatus*, showing rostral not curved over snout, upper preocular contacting postnasal, and anterior subocular touching fourth and fifth supralabials.

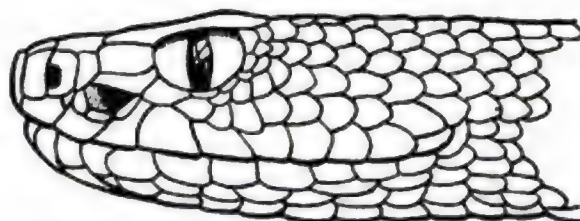


Fig. 2:99. *S. miliarius*, showing upper preocular separated from postnasal, and anterior subocular touching third and fourth supralabials.

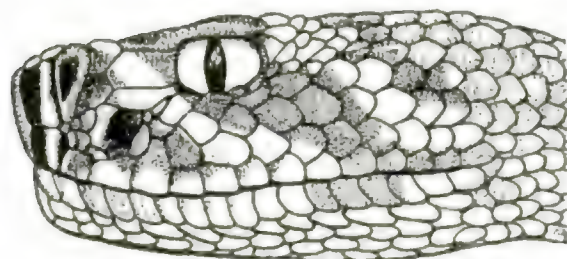


Fig. 2:100. *C. adamanteus*, showing vertical light marks on prenasal and first supralabial.

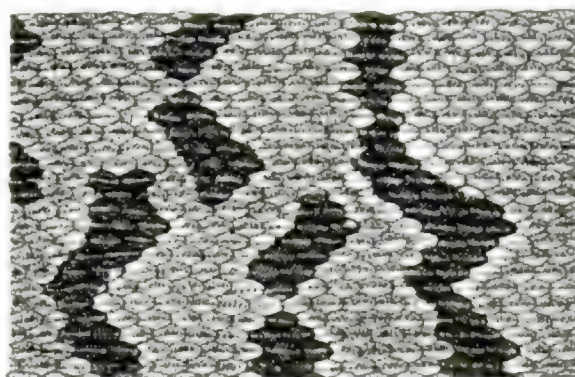


Fig. 2:101. Dorsal pattern of *C. h. horridus*.

KEY TO THE RATTLESNAKES OF THE UNITED STATES  
EAST OF THE MISSISSIPPI RIVER

- 1a. Top of the head with large, symmetrically arranged plates anteriorly, usually 9 in number (fig. 2:96) .....Genus *Sistrurus* 2
- 1b. Top of the head with small scales anteriorly (fig. 2:97) .....Genus *Crotalus* 5
- 2a. Upper preocular usually in contact with the postnasal (fig. 2:98); anterior subocular usually contacts the fourth and fifth supralabials; 11 or more dorsal scale rows at the center of the tail; no red or orange in the interblotch spaces on the middorsal line  
*Sistrurus catenatus catenatus* (fig. 2:76)
- 2b. Upper preocular not in contact with the postnasal (fig. 2:99); anterior subocular usually contacts the third and fourth supralabials; 10 or fewer dorsal scale rows at the center of the tail; usually with red or orange between blotches on the middorsal line  
*Sistrurus miliarius*  
(For subspecies continue on to 3)
- 3a. Dorsal coloration dark-gray to black; ventral surface white, heavily blotched with dark-brown or black; head markings obscure; lateral spots in 3 series. .*Sistrurus miliarius barbouri* (fig. 2:80)
- 3b. Dorsal coloration brown or light-gray; ventral surface cream, moderately flecked with brown or gray; head markings distinct; lateral spots in 1 or 2 series..... 4
- 4a. Dorsal scale rows usually 23; dorsal spots oval or subcircular, with even edges; lateral spots usually round; ventral spots usually occupying two adjacent scutes  
*Sistrurus miliarius miliarius* (fig. 2:79)
- 4b. Dorsal scale rows usually 21; dorsal spots wider than long and with irregular edges; lateral spots usually higher than wide; ventral spots confined to individual scutes  
*Sistrurus miliarius streckeri* (fig. 2:81)
- 5a. A vertical light line on the posterior edges of the prenasals and first supralabials (fig.2:100); a pattern of black or dark-brown diamonds, bordered by single rows of yellowish scales  
*Crotalus adamanteus* (fig. 2:11)
- 5b. No vertical light line on the posterior edges of the prenasals and first supralabials; a pattern comprising a series of crossbands or chevrons (fig.2:101), often irregular, or with the body all black .....*Crotalus horridus*  
(For subspecies continue on to 6)
- 6a. Dorsal scale rows usually 23; postocular dark stripe indistinct; body bands often dull, not sharply contrasting with the ground color, sometimes obscured by black  
*Crotalus horridus horridus* (fig. 2:30)
- 6b. Dorsal scale rows usually 25; postocular dark stripe distinct; body bands sharply contrasting with ground color, often outlined with light scales.  
*Crotalus horridus atricaudatus* (fig. 2:31)

KEY TO THE RATTLESNAKES OF THE UNITED STATES  
WEST OF THE MISSISSIPPI RIVER

- 1a. Top of the head with large plates anteriorly (usually 9 in number) including a single frontal and a pair of large, symmetrical parietals in contact with each other (fig. 2:96)  
Genus *Sistrurus* 2
- 1b. Top of the head with scales of varying size anteriorly; more than one scale in the frontal area; parietals, if enlarged, not in contact or symmetrical (fig. 2:97) .....Genus *Crotalus* 4
- 2a. Upper preocular not in contact with the postnasal (fig. 2:99); anterior subocular usually contacts the third and fourth supralabials; 10 or fewer dorsal scale rows at the center of the tail; usually with red or orange between blotches on the middorsal line  
*Sistrurus miliarius streckeri* (fig. 2:81)



Fig. 2:102. Ventral pattern of *S. c. catenatus*.

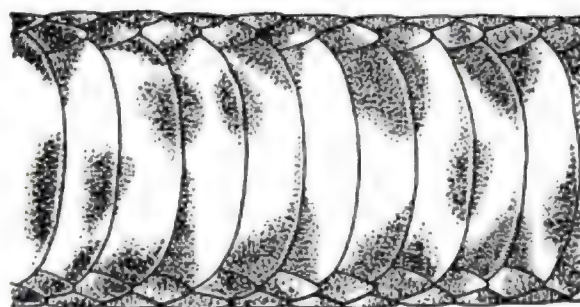


Fig. 2:103. Ventral pattern of *S. c. tergeminus*.

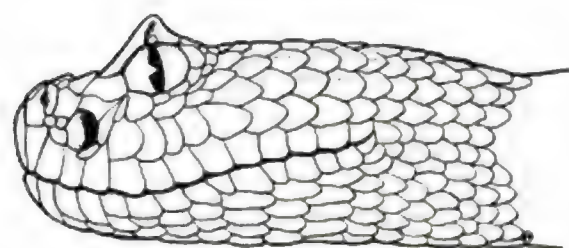


Fig. 2:104. *C. cerastes*, showing hornlike supraocular (lateral view).

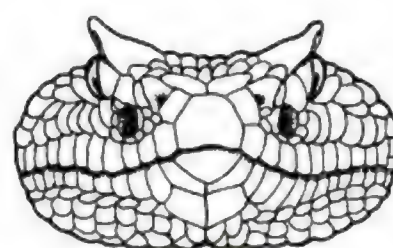


Fig. 2:105. *C. cerastes*, showing hornlike supraoculars (front view).

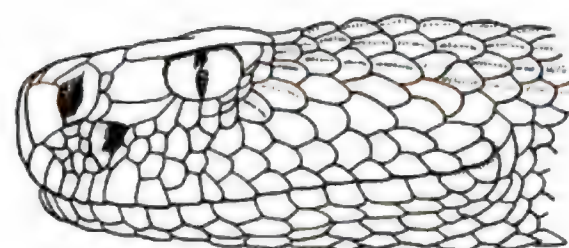


Fig. 2:106. Lateral head scales of *Crotalus* (*C. atrox*).

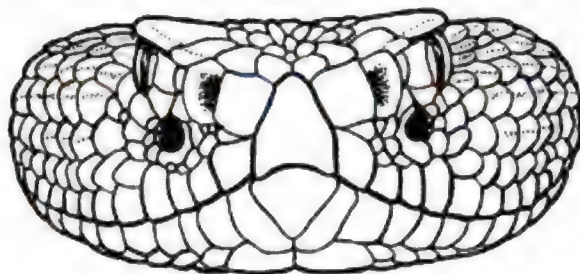


Fig. 2:107. Head scales of *Crotalus* (*C. atrox*) (front view).

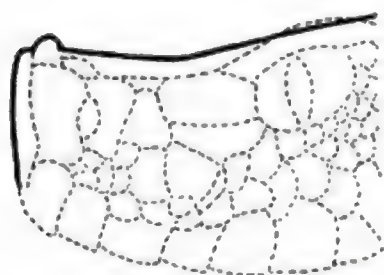


Fig. 2:108. Cross section of head of *C. willardi*, showing internasal ridge.

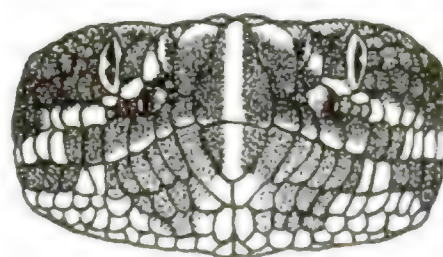


Fig. 2:109. Head of *C. w. willardi*, showing light line present on rostral and mental.

- 2b. Upper preocular usually in contact with the postnasal (fig. 2:98); anterior subocular usually contacts the fourth and fifth supralabials; 11 or more dorsal scale rows at the center of the tail; no red or orange in the interblotch spaces on the middorsal line
- Sistrurus catenatus
- (For subspecies continue on to 3)
- 3a. Undersurface dark, heavily clouded with black blotches, often almost solid black (fig. 2:102); mid-body scale rows usually 25; body blotches usually fewer than 37
- Sistrurus catenatus catenatus (fig. 2:76)
- 3b. Undersurface mottled, spotted, or immaculate, the dark areas being less extensive than the light; mid-body scale rows 23 or 25; body blotches usually more than 36.....4
- 4a. Undersurface mottled or considerably spotted (fig. 2:103); mid-body scale rows usually 25
- Sistrurus catenatus tergeminus (fig. 2:78)
- 4b. Undersurface lightly spotted or immaculate; mid-body scale rows usually 23
- Sistrurus catenatus edwardsii (fig. 2:77)
- 5a. Outer edges of the supraoculars extended into raised and flexible hornlike processes distinctly pointed at the tip (figs. 2:104 and 2:105) .....Crotalus cerastes
- (For subspecies continue on to 6)
- 5b. Outer edges of the supraoculars not extended into pointed hornlike processes (figs. 2:106 and 2:107) ..... 8
- 6a. Proximal lobe of the rattle-matrix brown in adults...Crotalus cerastes cerastes (fig. 2:16)
- 6b. Proximal lobe of the rattle-matrix black in adults ..... 7
- 7a. Mid-body scale rows usually 23; ventrals in the males more than 141; in the females more than 145.....Crotalus cerastes laterorepens (fig. 2:18)
- 7b. Mid-body scale rows usually 21; ventrals in the males 141 or fewer; in the females 145 or fewer.....Crotalus cerastes cercobombus (fig. 2:17)
- 8a. Tip of the snout and the anterior canthus rostralis raised into a sharp ridge (fig. 2:108)
- Crotalus willardi
- (For subspecies continue on to 9)
- 8b. Tip of the snout and the anterior canthus rostralis not raised into a sharp ridge (fig. 2:110) .....10
- 9a. A white vertical line on the rostral and mental (fig. 2:109)...Crotalus willardi willardi (fig. 2:72)
- 9b. No white vertical line on the rostral or mental.....Crotalus willardi silus (fig. 2:75)

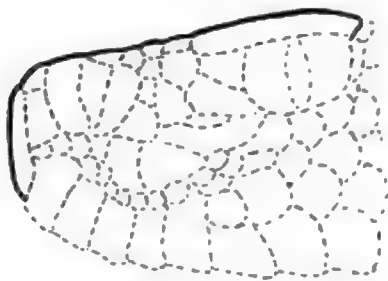


Fig. 2:110. Cross section of head of *Crotalus*, showing absence of internasal ridge.

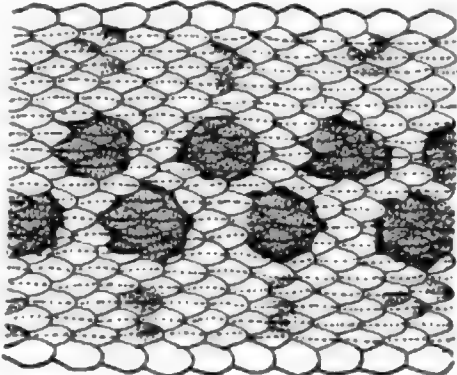


Fig. 2:111. Dorsal pattern of *C. p. pricei*, showing twin rows of spots.

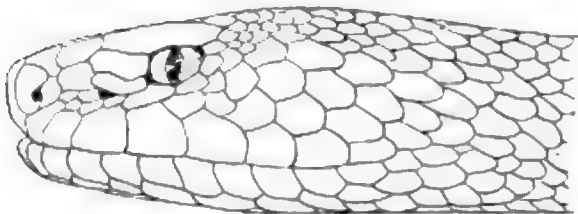


Fig. 2:112. Head of *C. p. pricei*, showing broad contact between postnasal and first supralabial, and anterior subocular touching third and fourth supralabials.

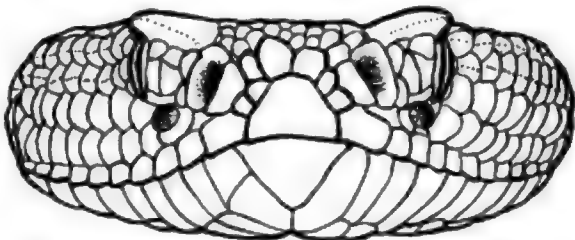


Fig. 2:113. *C. mitchellii pyrrhus* (front view), showing separation of rostral from prenasals, and rostral wider than high.

- 10a. Postnasal in broad contact with the first supralabial (fig. 2:112); anterior subocular in contact with the third and fourth supralabials; mid-body scale rows plus supralabials on both sides of the head total 41 or fewer; a dorsal pattern usually comprised of two rows of small brown spots on opposite sides of the middorsal line (fig. 2:111), but some or many of which spots may be joined together middorsally. *Crotalus pricei pricei* (fig. 2:47)
- 10b. Postnasal usually separated from the first supralabial, or, if in contact, only to a small extent; anterior subocular not in contact with the third and fourth supralabials; mid-body scale rows plus supralabials on both sides of the head total 42 or more; dorsal pattern not comprised of two rows of small brown spots on opposite sides of the middorsal line ..... 11
- 11a. Prenasals usually separated from the rostral by small scales or granules<sup>43</sup> (fig. 2:113), or, at least, the front edges of the prenasals chipped and sutured  
*Crotalus mitchellii pyrrhus* (fig. 2:41)
- 11b. Prenasals contacting the rostral, and their front edges not chipped or sutured (fig. 2:107) . 12
- 12a. Upper preocular usually split vertically, the anterior section being higher than the posterior and curved over the canthus rostralis in front of the supraocular (fig. 2:114); usually a pattern of widely separated brown blotches or crossbars on a tan, light-brown, gray, green, or blue-green background (fig. 2:115) ..... *Crotalus lepidus*  
(For subspecies continue on to 13)
- 12b. Upper preocular not split vertically; or if split, the anterior section not conspicuously higher than the posterior and not curved over the canthus rostralis in front of the supraocular; the anterior pattern not of widely separated cross bars or rings; or, if there are bars, the tail is all black..... 14
- 13a. A dark stripe passing backward from the eye to the angle of the mouth (fig. 2:114); a pair of separated occipital blotches; the dorsal pattern of blotches or crossbars often not strongly differentiated from the ground color and with intermediate blotches almost as conspicuous as the major series..... *Crotalus lepidus lepidus* (fig. 2:35)
- 13b. Postocular dark stripe obsolescent or absent in adults; occipital blotches confluent; the dorsal pattern of dark blotches or crossbars sharply contrasting with the lighter ground color; intermediate blotches usually reduced to scattered black scale tips (fig. 2:115)  
*Crotalus lepidus klauberi* (fig. 2:36)
- 14a. A vertical light line on the posterior edges of the prenasals and first supralabials (fig. 2:100)  
*Crotalus adamanteus* (fig. 2:11)
- 14b. No vertical light line on the posterior edges of the prenasals and first supralabials. . . . 15

<sup>43</sup> About 17 per cent of the specimens of *C. viridis cerberus* have this rostral-prenasal separation, which is here used to identify *C. mitchellii pyrrhus*. If the specimen is from Arizona and has a black, dark-brown, or dark-gray ground color, rather than cream, tan, pink, light-gray, or light-brown, then it is *C. v. cerberus* and not *C. m. pyrrhus*, even if the prenasals are separated, or almost separated, from the rostral by the interposition of a row of small scales.

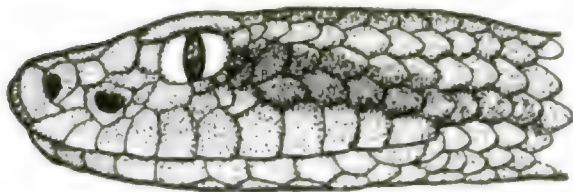


Fig. 2:114. *C. l. lepidus*, showing split upper preocular, prenasal curved under postnasal, and ocular dark stripe.

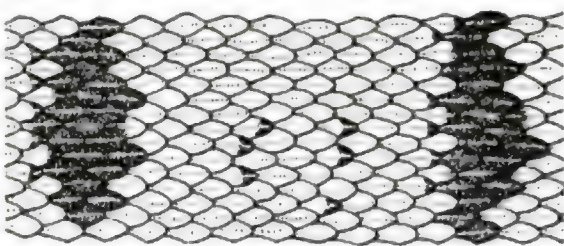


Fig. 2:115. Dorsal pattern of *C. l. klauberi*.

- 15a. More than two internasals—that is, scales between the nasals and in contact with the rostral, regardless of their size or position<sup>44</sup> (fig. 2:116) ..... *Crotalus viridis*  
(For subspecies continue on to 16)
- 15b. Two internasals (fig. 2:117) ..... 23
- 16a. Light postocular stripe 1 or 1½ scales wide and clearly outlined (fig. 2:118); body blotches commonly subrectangular, with even edges and usually with a narrow, light border (fig. 2:120) ..... 17
- 16b. Light postocular stripe 2 or more scales wide (fig. 2:119), often indefinite or absent, especially in adults; body blotches, if in evidence, commonly diamonds or ellipses, or if rectangles, with edges rough or serrated, and often without narrow light borders.... 18

<sup>44</sup> Some specimens of *Crotalus viridis* have only two internasals and thus would fail to key out properly by the use of this character. *C. v. oregonus* is the worst defaulter, for of this subspecies about 14 per cent have only two internasals. To avoid taking the wrong course, one may reinforce the decision by proceeding to 16 regardless of the number of internasals, if the snake is from central or northern California west of the Sierra Nevada, from Oregon, Washington, Idaho, northern Nevada, Utah (except the extreme southwestern corner), Colorado, Wyoming, Montana, the Dakotas, western Nebraska, or western Kansas.

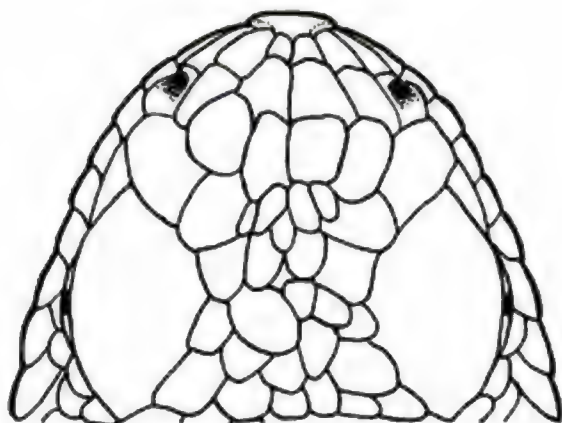


Fig. 2:116. Crown of *Crotalus*, showing four internasals.

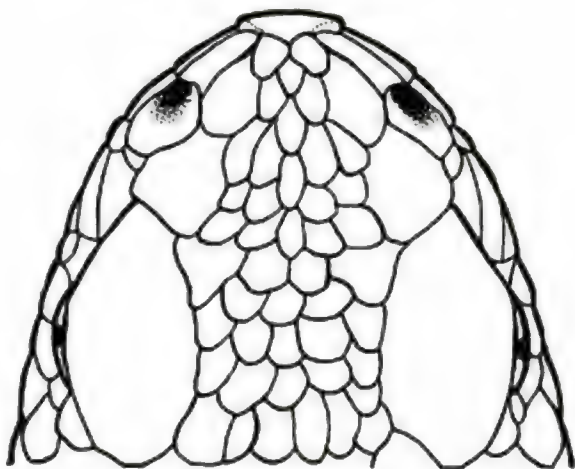


Fig. 2:117. Crown of *Crotalus*, showing two internasals.



Fig. 2:118. Lateral head pattern of *C. v. viridis*.



Fig. 2:119. Lateral head pattern of *C. v. helleri*.

- 17a. Color usually green or olive-green, less often olive-brown or brown; scale rows 27 or 25; dorsal scale rows at the center of the tail 13 or more; adult size exceeding 850 mm.  
*Crotalus viridis viridis* (fig. 2:62)
- 17b. Color pink, red, or red-brown; scale rows 25 or 23; dorsal scales at the center of the tail 12 or fewer; adult size rarely exceeding 650 mm.....*Crotalus viridis nuntius*<sup>45</sup> (fig. 2:69)
- 18a. Color straw, cream, or yellow; blotches often only faintly in evidence or obsolete in adults; adult size smaller, usually under 650 mm....*Crotalus viridis concolor* (fig. 2:66)
- 18b. Color darker, not straw, cream, or yellow; adult size larger, over 650 mm.....19
- 19a. Adult color vermilion or salmon; body blotches tending toward obsolescence in adults  
*Crotalus viridis abyssus*<sup>45</sup> (fig. 2:63)
- 19b. Adult color other than vermilion or salmon; body blotches in evidence or body black...20

<sup>45</sup> The great variability in the colors of the subspecies of *C. viridis* renders it desirable to reinforce these identifications by recourse to localities. *C. v. nuntius* is found only in the Little Colorado-Painted Desert area of Arizona; *C. v. concolor* only in the Colorado and Green rivers drainage area of eastern Utah, southwestern Wyoming, and western Colorado; and *C. v. abyssus* only in the Grand Canyon and along its borders in Arizona. All these areas comprise parts of the drainage basin of the upper Colorado River; if the snake to be checked is from outside this drainage basin, it may be identified as *C. v. viridis*, if the postocular light stripe is narrow (fig. 2:118), or proceed forward to 20 if it is wide (fig. 2:119), poorly outlined, or absent. This footnote is applicable only if course 16 (rather than 23) was taken at 15.

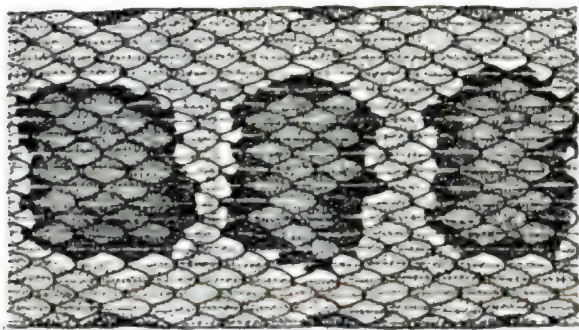


Fig. 2:120. Dorsal pattern of *C. v. viridis*.

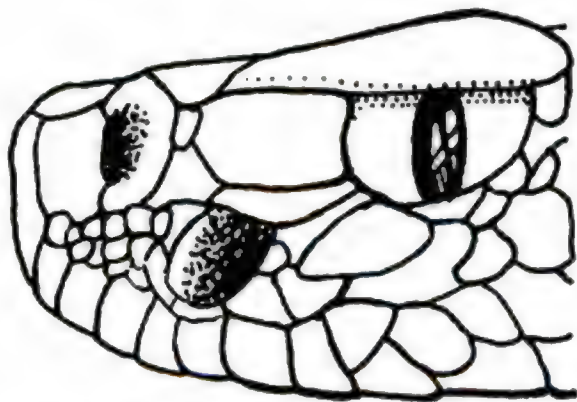


Fig. 2:121. Snout of *Crotalus*, showing upper loreal present, and no contact between prenasal and first supralabial.

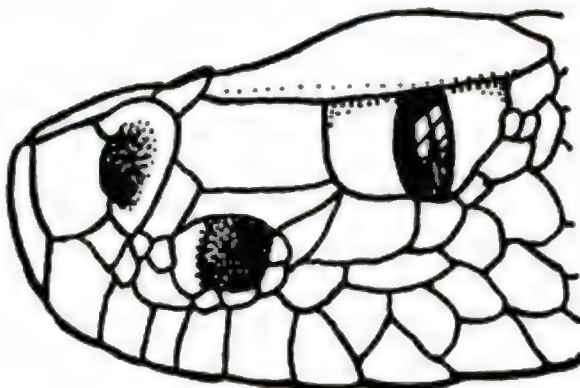


Fig. 2:122. Snout of *Crotalus*, showing contact between postnasal and upper preocular, and between prenasal and first supralabial.

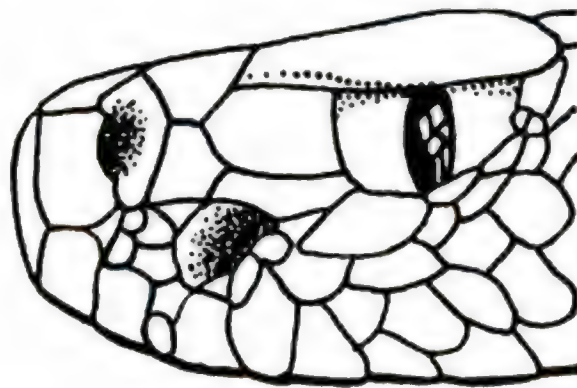


Fig. 2:123. Snout of *Crotalus*, showing contact between postnasal and upper preocular, prevented by junction of canthal with loreal.

- 20a. Ground color lighter, usually buff or drab; body blotches occupy less or but little more longitudinal space than the interspaces; secondary series of lateral blotches little in evidence; a pattern of dark-brown dorsal blotches (often with light centers) on a buff or drab ground color.....*Crotalus viridis lutosus* (fig. 2:68)
- 20b. Ground color darker, usually dark-gray, olive, brown, or black; dark-brown or black dorsal blotches (usually diamonds or hexagons) occupying considerably more longitudinal space than the interspaces; a secondary series of lateral blotches conspicuously in evidence. Some mountain specimens nearly uniform black, only patches of yellow scales representing the interspaces on the middorsal line.....21
- 21a. Loreals usually two; usually one or more scales at the rostral between the prenasal and the first supralabial (fig. 2:121) .....*Crotalus viridis cerberus* (fig. 2:65)
- 21b. Loreals usually single; usually no scales between the prenasal and the first supralabial at the rostral (fig. 2:122) .....22
- 22a. Last dark tail ring about twice as wide as the others and ill defined (yellow in juveniles) .....*Crotalus viridis helleri* (fig. 2:67)
- 22b. Dark tail rings of uniform width and all clearly defined  

*Crotalus viridis oreganus* (figs. 2:70 and 2:71)
- 23a. Supraoculars pitted, sutured, or with outer edges broken (fig. 2:124)  

*Crotalus mitchellii stephensi* (fig. 2:42)
- 23b. Supraoculars unbroken .....24
- 24a. Tail rings absent or only obscurely distinguishable from the ground color owing to lack of contrast; tail often very dark-brown, dark-gray, or entirely black.....25
- 24b. Light and dark alternating tail rings clearly evident, usually black or brown on a light-gray or tan ground color (fig. 2:126) .....27

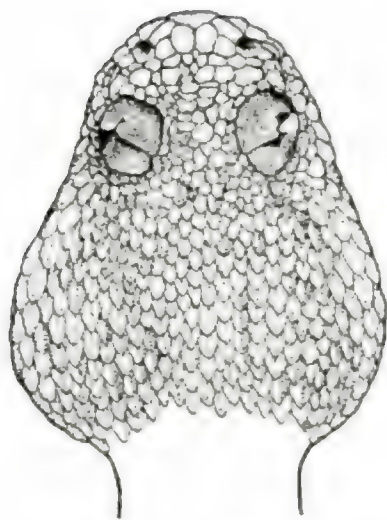


Fig. 2:124. *C. m. stephensi*, showing sutured supraoculars.

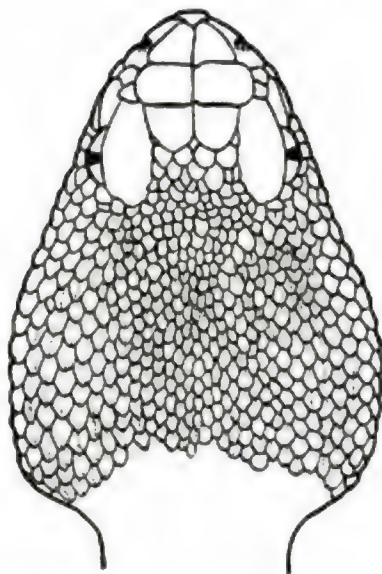


Fig. 2:125. Head of some species of *Crotalus* exemplifying full-sized internasals and prefrontals, and enlarged scales in anterior part of frontal area.

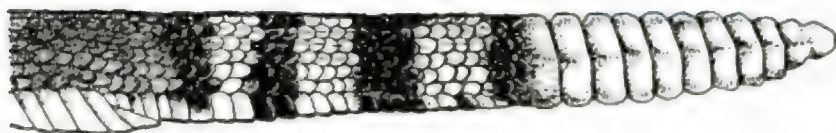


Fig. 2:126. Tail pattern of *atrox* group.

- 25a. Ventrals rarely fewer than 180; supralabials rarely 15 or fewer; usually 8 or fewer large flat scales in the internasal-prefrontal area; usually a straight dividing line or suture between the scales in the internasal and prefrontal areas; scales in the anterior part of the frontal area larger than those behind (fig. 2:125); body pattern comprising diamonds, which posteriorly are open laterally (fig. 2:127) ..... *Crotalus molossus molossus* (fig. 2:43)
- 25b. Ventrals rarely more than 179; supralabials rarely more than 15; usually more than 8 scales in the internasal-prefrontal region; no definite division or straight suture between the scales of the frontal and prefrontal areas; scales in the anterior part of the frontal area not conspicuously larger than those behind (fig. 2:129); body pattern comprising irregular crossbands or chevrons (fig. 2:101), in some specimens obscured by a black suffusion. . . . *Crotalus horridus*  
(For subspecies continue on to 26)
- 26a. Dorsal scale rows usually 23; postocular dark stripe indistinct; body bands often dull, not sharply contrasting with the ground color, sometimes obscured by black  
..... *Crotalus horridus horridus* (fig. 2:30)
- 26b. Dorsal scale rows usually 25; postocular dark stripe distinct; body bands sharply contrasting with the ground color; often outlined with light scales  
..... *Crotalus horridus atricaudatus* (fig. 2:31)
- 27a. A definite division between the scales of the prefrontal and frontal areas; minimum scales between the supraoculars rarely more than 2; each supraocular bordered inwardly and posteriorly by a large flat crescentic scale (fig. 2:130) . . . *Crotalus scutulatus scutulatus* (fig. 2:53)
- 27b. No definite division between the scales of the prefrontal and frontal areas; minimum scales between the supraoculars rarely less than 4; no large, flat crescentic scales behind the supraoculars (fig. 2:97) ..... 28
- 28a. Tail usually of alternating brown and tan rings not in sharp contrast with the posterior body color ..... *Crotalus tigris* (fig. 2:56)
- 28b. Tail of alternating black and light ash-gray rings, both colors in sharp contrast with the posterior body color (fig. 2:126) ..... 29
- 29a. Body color predominantly cream, buff, gray, or gray-brown<sup>46</sup>, with dark dots conspicuous in the body blotches; scale rows most often 25; minimum scales between supraoculars usually 5 or less; first infralabials rarely divided transversely (fig. 2:131)<sup>47</sup>. . . *Crotalus atrox* (fig. 2:12)
- 29b. Body color predominantly pink, red, brick-red, or red-brown, without conspicuous dark dots in the body blotches; scale rows most often 29; minimum scales between supraoculars usually 6 or more; first infralabials usually divided transversely (fig. 2:132)  
..... *Crotalus ruber ruber* (figs. 2:50 and 2:51)

<sup>46</sup> May be pink or red in New Mexico, but *ruber* does not occur in that state, or anywhere else in the United States except in southern California.

<sup>47</sup> Many California specimens of *atrox* have divided first infralabials, which is unfortunate for the herpetologist since this is the only state in which a key is necessary to separate *atrox* and *ruber*, for the latter is found in no other state.

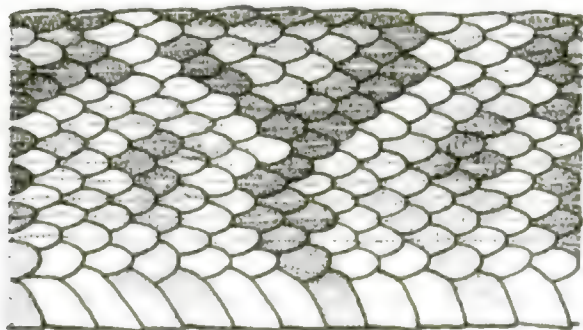


Fig. 2:127. Lateral pattern of *C. m. molossus*.

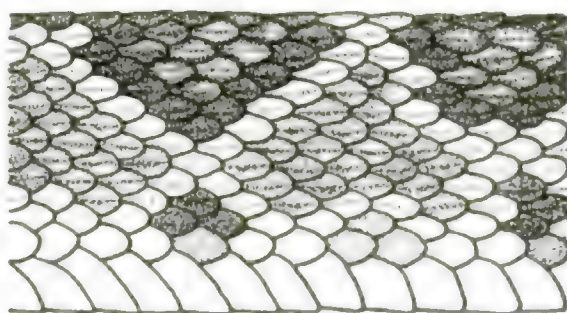


Fig. 2:128. Lateral pattern of some species of *Crotalus* exemplifying dark interior blotch border, light exterior blotch border (with unicolored scales), and intermediate lateral ground color in the interspaces.

# KEY TO THE RATTLESNAKES OF MEXICO

(Exclusive of Baja California and the Islands of the Gulf of California and of the Pacific Coast)

- 1a. Top of the head with large plates anteriorly (usually 9 in number) including a single frontal and a pair of large, symmetrical (but sometimes sutured) parietals in contact (fig. 2:96)  
Genus *Sistrurus* 2
- 1b. Top of the head with scales of varying sizes; more than one scale in the frontal area; parietals, if enlarged, not in contact or symmetrical (fig. 2:97) ..... Genus *Crotalus* 3
- 2a. Upper preocular not in contact with the postnasal; rostral curved over the snout; canthus rostralis rounded (fig. 2:133); dorsal body blotches longer than wide (fig. 2:135) or color black.....*Sistrurus rarus* (fig. 2:82)
- 2b. Upper preocular in contact with the postnasal; rostral not curved over the snout (fig. 2:98); canthus rostralis sharply angled; dorsal body blotches square or wider than long  
*Sistrurus catenatus edwardsii*<sup>4</sup> (fig. 2:77)
- 3a. Outer edges of the supraoculars extended into raised and flexible hornlike processes distinctly pointed at the tip (figs. 2:104 and 2:105) .....*Crotalus cerastes*  
(For subspecies continue on to 4)
- 3b. Outer edges of the supraoculars not extended into pointed hornlike processes (figs. 2:106 and 107) .....5
- 4a. Mid-body scale rows usually 21; ventrals in the males 141 or fewer; in the females 145 or fewer.....*Crotalus cerastes cercobombus* (fig. 2:17)
- 4b. Mid-body scale rows usually 23; ventrals in the males more than 141; in the females more than 145.....*Crotalus cerastes laterorepens* (fig. 2:18)
- 5a. Subcaudals in males more than 40, and in females more than 35.....39
- 5b. Subcaudals in males fewer than 40, and in females fewer than 35.....6
- 6a. Tip of the snout and the anterior canthus rostralis raised into a sharp ridge (fig. 2:108)  
*Crotalus willardi*  
(For subspecies continue on to 7)
- 6b. Tip of the snout and the anterior canthus rostralis not raised into a sharp ridge (fig. 2:110) ..... 9
- 7a. No white vertical line on the rostral or mental.....*Crotalus willardi silus* (fig. 2:75)
- 7b. A white vertical line on the rostral and mental (fig. 2:109) .....8
- 8a. Body blotches 35 or more.....*Crotalus willardi amabilis* (fig. 2:73)
- 8b. Body blotches 34 or fewer.....9
- 9a. Scale rows usually 25; subcaudals 29 or fewer in the males and 26 or fewer in the females; body blotches 26 or fewer.....*Crotalus willardi willardi* (fig. 2:72)
- 9b. Scale rows usually more than 25; subcaudals 30 or more in the males and 27 or more in the females; body blotches more than 26.....*Crotalus willardi meridionalis* (fig. 2:74)
- 10a. Prenasals separated from the rostral by small scales or granules (fig. 2:113)  
*Crotalus mitchellii pyrrhus* (fig. 2:41)
- 10b. Prenasals contacting the rostral (fig. 2:107) .....11
- 11a. Body pattern comprises a series of 35 or more crossbands composed of conspicuous dark-gray or brown dots on a buff, pink, or light-gray background; dorsoventral width of proximal rattle contained in the head length less than 2½ .....*Crotalus tigris* (fig. 2:56)
- 11b. Body pattern comprises diamonds, hexagons, rectangles, ovals, or ellipses, or, if bands, not made up of conspicuous dots; dorsoventral width of proximal rattle contained in the head length more than 2½ times.....12
- 12a. Anterior subocular contacts one or more (usually 2) supralabials.....13

<sup>4</sup> No unquestionably accurate records of this snake in Mexico are known, all reports thus far being subject to some doubt. However, occurrence south of the United States border is not improbable.

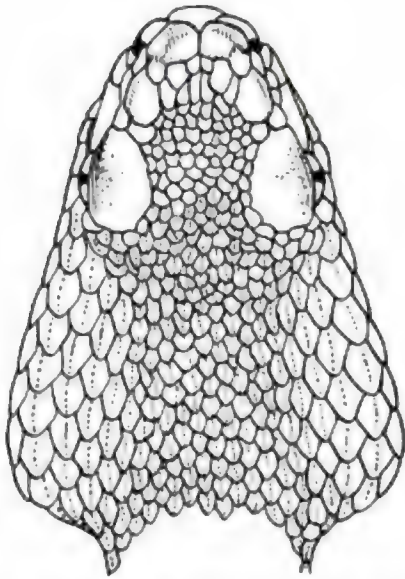


Fig. 2:129. Dorsal head scales of some species of *Crotalus* exemplifying a breakup of scales in the internasal, prefrontal, and frontal areas.

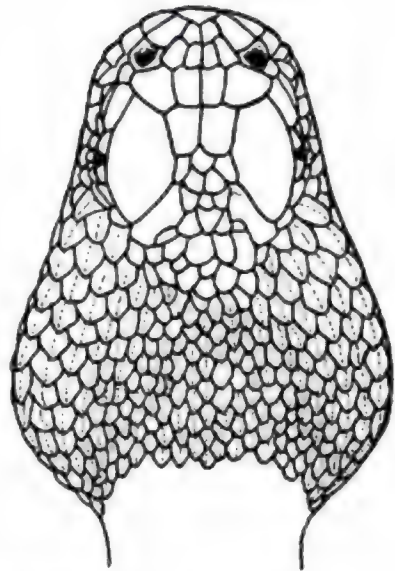


Fig. 2:130. Dorsal head scales of *C. scutulatus*, showing paired anterior intersupraoculars, and enlarged crescentic scales bordering the supraoculars inwardly behind.

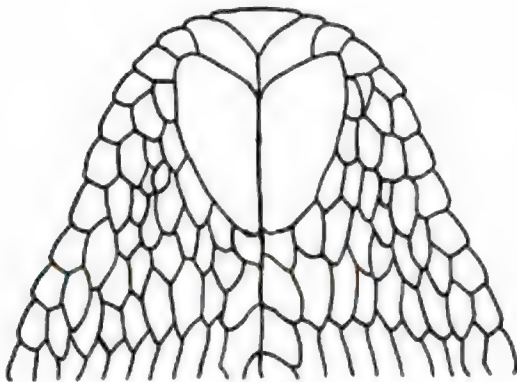


Fig. 2:131. Chin shields of *Crotalus*; first infralabials undivided.

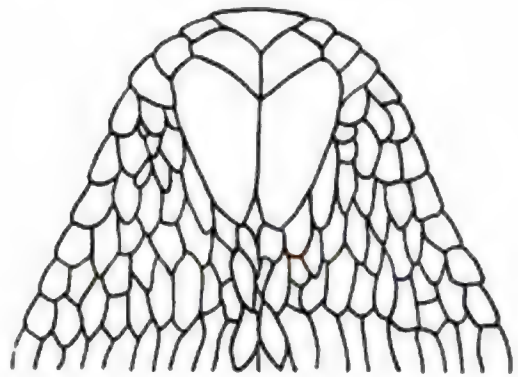


Fig. 2:132. Chin shields of *Crotalus*; first infralabials divided.

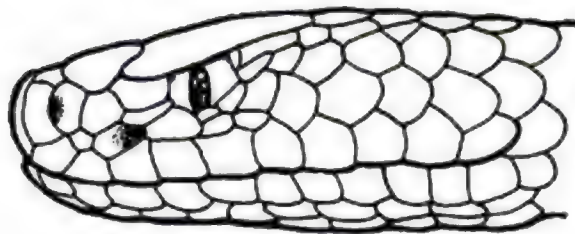


Fig. 2:133. *S. ravus*, showing rostral curved over snout.



Fig. 2:134. *C. polystictus*, showing backwardly curved supraocular light line, and paired and elongated intercanthals.

- 12b. Anterior subocular fails to reach any supralabial.....24
- 13a. Each supraocular transversely crossed by a thin, black-bordered light line that usually bends backward outwardly (fig. 2:134); a clearly outlined round or oval dark blotch immediately below and touching the eye; dorsal pattern usually comprised of longitudinal ellipses (fig. 2:136); usually a pair of slim intercanthals, each about twice as long as wide (fig. 2:134)
- Crotalus polystictus*
- 13b. No thin, black-bordered transverse lines on the supraoculars; no clearly outlined round or oval blotch immediately below the eye; intercanthals, if paired, not long and slim.....14
- 14a. Mid-body scale rows plus the supralabials on both sides of the head total 41 or fewer.15
- 14b. Mid-body scale rows plus the supralabials on both sides of the head total 42 or more.20
- 15a. Loreal in contact with one or more supralabials (fig. 2:138) .....*Crotalus intermedius*  
(For subspecies continue on to 16)
- 15b. Loreal not in contact with any supralabial.....18
- 16a. Ventrals 163 or fewer in the males, and 169 or fewer in the females.....17
- 16b. Ventrals 164 or more in the males, and 170 or more in the females
- Crotalus intermedius omiltemanus* (fig. 2:34)
- 17a. Broad contact between the first supralabial and the postnasal, which usually touches no other supralabial.....*Crotalus intermedius gloydi* (fig. 2:33)
- 17b. Postnasal touches both the first and second supralabials, the first usually broadly, the second narrowly.....*Crotalus intermedius intermedius* (fig. 2:32)
- 18a. Lower preocular passes into the pit and fails to make a full contact with the loreal (fig. 2:138); a dorsal pattern of transverse bars, undivided middorsally.. *Crotalus transversus*

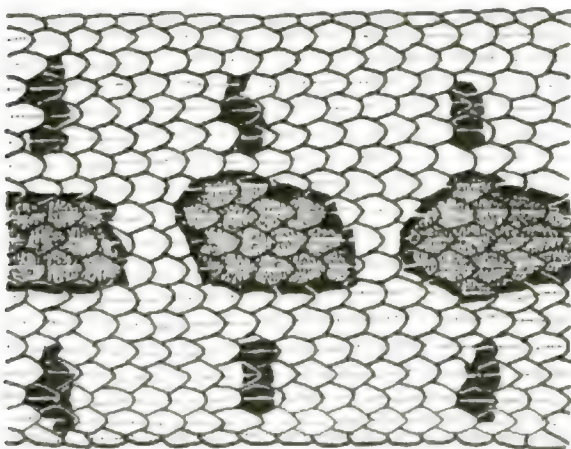


Fig. 2:135. Dorsal pattern of *S. ravus*.

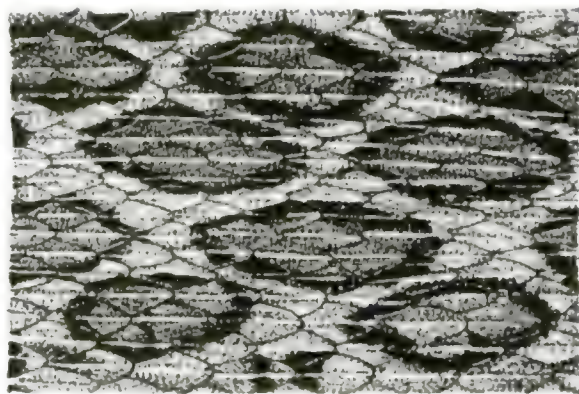


Fig. 2:136. Dorsal pattern of *C. polystictus*.

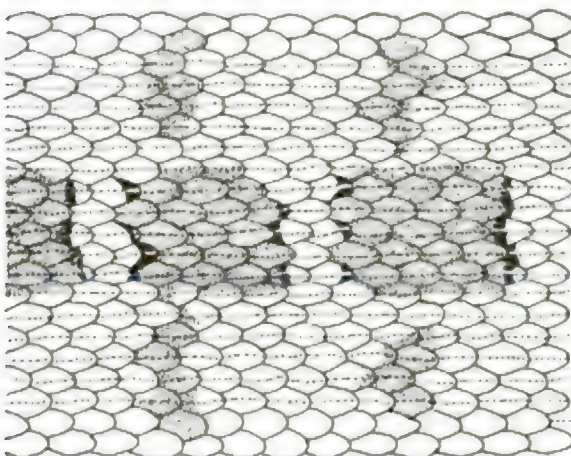


Fig. 2:137. Dorsal pattern of *C. t. aquilus*, showing undivided blotches.

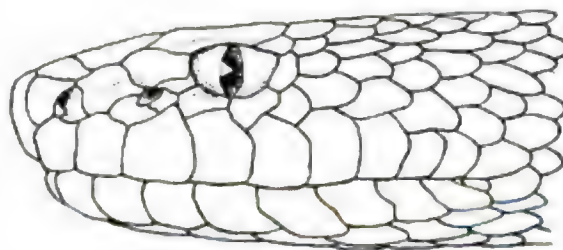


Fig. 2:138. *C. intermedius*, exemplifying contact of loreal with a supralabial, loreal with prenasal, and lack of contact between loreal and lower preocular.

## 130 *Classification and Identification*

- 18b. Lower preocular passes above the pit and makes a contact with the loreal; the dorsal pattern often comprised largely or to some extent of two rows of small blotches on opposite sides of the middorsal line (fig. 2:111) <sup>49</sup>.....*Crotalus pricei*  
(For subspecies continue on to 19)
- 19a. Ventrals 147 or more.....*Crotalus pricei pricei* (fig. 2:47)
- 19b. Ventrals 146 or fewer.....*Crotalus pricei miquihuanus* (fig. 2:48)
- 20a. Prefrontals (canthals) paired and in contact, and with even but convex posterior edges  
*Crotalus pusillus* (fig. 2:49)
- 20b. More than 2 scales in the prefrontal area.....21
- 21a. Upper preocular usually split vertically, the anterior section being higher than the posterior and curved over the canthus rostralis in front of the supraocular (fig. 2:114); dorsal body blotches occupy less longitudinal space than the interspaces (fig. 2:115); primary dorsal body blotches or crossbands seldom exceed 24 except in Tamaulipas.....*Crotalus lepidus* <sup>50</sup>  
(For subspecies continue on to 22)
- 21b. Upper preocular not split vertically (fig. 2:139); or, if split, the anterior section not conspicuously higher than the posterior and not curved over the canthus rostralis in front of the supraocular; dorsal body blotches occupy more longitudinal space than the interspaces; primary dorsal body blotches usually exceed 24.....*Crotalus triseriatus*  
(For subspecies continue on to 28)
- 22a. Primary dorsal body blotches or crossbands 25 or more.....*Crotalus lepidus morulus*
- 22b. Primary dorsal body blotches or crossbands fewer than 25.....23
- 23a. A dark stripe passing backward from the eye to the angle of the mouth (fig. 2:114); a pair of separated occipital blotches; the dorsal pattern of blotches or crossbars often not strongly differentiated from the ground color and the intermediate blotches almost as prominent as the major series.....*Crotalus lepidus lepidus* (fig. 2:35)
- 23b. Postocular dark stripe obsolescent or absent (except in juveniles); occipital blotches confluent; the dorsal pattern of dark blotches or crossbars strongly differentiated from the ground color (fig. 2:115).....*Crotalus lepidus klauberi* <sup>51</sup> (fig. 2:36)

<sup>49</sup> See footnote 24 under *C. p. miquihuanus*.

<sup>50</sup> It has been necessary to double-key *lepidus*, as the anterior subocular sometimes contacts one or more labials and sometimes does not. The same is true of *triseriatus*, although this contact fails in the latter form much less often than in *lepidus*. I have not double-keyed *pusillus*, although in a specimen from Nayarit the anterior subocular fails to reach the supralabials.

<sup>51</sup> See footnote 19.

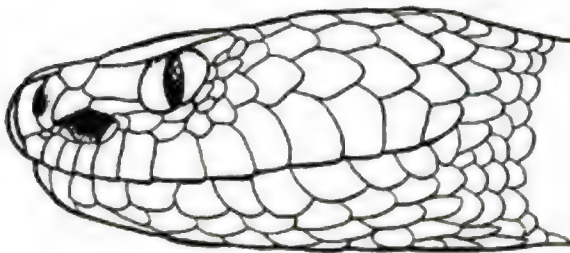


Fig. 2:139. Lateral head scales of *C. t. triseriatus*.

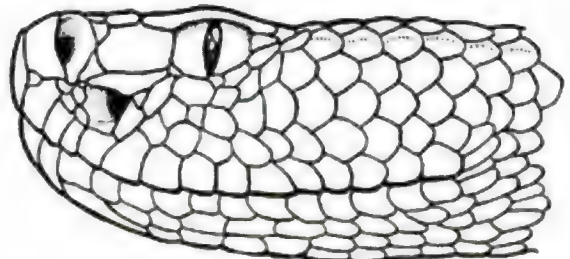


Fig. 2:140. Lateral head scales of *C. b. basiliscus*, exemplifying presence of a postrostral.

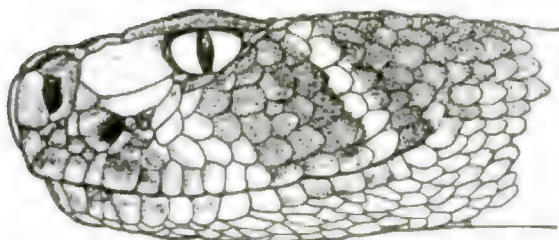


Fig. 2:141. *C. atrox*, showing lateral head marks, with postocular light stripe intersecting the supralabials.

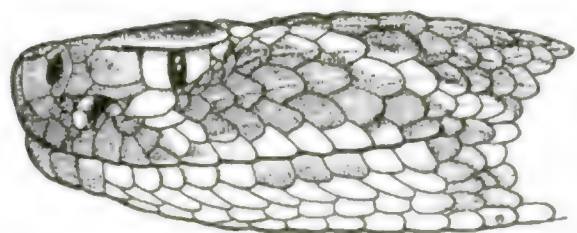


Fig. 2:142. *C. s. scutulatus*, showing lateral head marks, with postocular light stripe passing above angle of the mouth.

- 24a. More than two internasals—that is, scales between the nasals and in contact with the rostral, regardless of size or position (fig. 2:116) ..... *Crotalus viridis*  
(For subspecies continue on to 25)
- 24b. Two internasals (fig. 2:117) ..... 26
- 25a. Pattern of brown blotches on a tan or buff background; lightly mottled with brown below  
*Crotalus viridis viridis* (fig. 2:62)
- 25b. Pattern of dark-brown or black blotches on a dark-gray, dark-brown, or almost black background; heavily mottled with dark-brown or black below. *Crotalus viridis cerberus*<sup>52</sup> (fig. 2:65)
- 26a. Upper preocular usually split vertically; the anterior section being higher than the posterior and curved over the canthus rostralis in front of the supraocular (fig. 2:114), dorsal body blotches occupy less longitudinal space than the interspaces; pattern usually of blotches or crossbars (fig. 2:115) seldom exceeding 24 in number. .... *Crotalus lepidus*<sup>53</sup>  
(For subspecies drop back to 22)
- 26b. Upper preocular not split vertically (fig. 2:139); or, if split, the anterior section not conspicuously higher than the posterior and not curved over the canthus rostralis in front of the supraocular; dorsal body blotches occupy more longitudinal space than the interspaces; pattern of diamonds, hexagons, rectangles, or ellipses usually exceeding 24 in number. .... 27
- 27a. Ventral scales 163 or fewer. .... *Crotalus triseriatus*  
(For subspecies continue on to 28)
- 27b. Ventral scales 164 or more. .... 29
- 28a. Rattle-fringe scales usually 8; rattle smaller; in snakes exceeding 400 mm. in length, the dorsoventral width of the proximal rattle lobe is less than one per cent of the over-all body length; in snakes less than 400 mm. in length, the width of the proximal rattle lobe plus 1 mm. is less than 0.0075 times the body length  
*Crotalus triseriatus triseriatus* (fig. 2:58)
- 28b. Rattle-fringe scales usually 10; rattle larger; in snakes exceeding 400 mm. in length, the dorsoventral width of the proximal rattle lobe exceeds one per cent of the over-all body length; in snakes less than 400 mm. in length, the width of the proximal rattle lobe plus 1 mm. exceeds 0.0075 times the body length. *Crotalus triseriatus aquilus* (fig. 2:59)
- 29a. Tail rings contrasting, alternating white or light-gray with brown or black (fig. 2:126); at least 8, and usually more, scales occupying the internasal-prefrontal area (fig. 2:97) ..... 30
- 29b. Tail black or dark-gray, with rings, if present, only moderately evident, because of lack of contrast between the light and dark areas; usually 4 (fig. 2:125) or less often 6 or more large flat scales or plates occupying the internasal-prefrontal area (not including subcanthals or supralorals) ..... 32
- 30a. Light and dark tail rings of approximately equal widths; the postocular light stripe, if present, reaches the supralabials 1 to 3 scales in advance of the angle of the mouth (fig. 2:141); minimum scales between the supraoculars rarely less than 4; no flat crescentic scale bordering each supraocular posteriorly (fig. 2:97) .... *Crotalus atrox* (fig. 2:12)
- 30b. Dark tail rings narrower than the light; the postocular light stripe, if present, passes backward above the angle of the mouth (fig. 2:142); minimum scales between the supraoculars usually 2, rarely more than 3; usually a flat crescentic scale bordering each supraocular on the posterior-inward side (fig. 2:130) ..... *Crotalus scutulatus*  
(For subspecies continue on to 31)
- 31a. Dorsal blotches usually bordered by a row of light, unicolored scales (fig. 2:128); dark postocular stripe extended as far as the angle of the mouth or beyond (fig. 2:142); distal dark tail rings distinctly darker than the body blotches, usually black; upper part of proximal lobe of the rattle matrix black (except in juveniles). *Crotalus scutulatus scutulatus* (fig. 2:53)
- 31b. Dorsal blotches usually not bordered by a row of light unicolored scales; dark postocular stripe not extending as far as the angle of the mouth; distal dark tail rings not in sharp con-

<sup>52</sup> It is very doubtful that this subspecies occurs in mainland Mexico, for there is only one highly questionable record to date. If it is found in Mexico, it will be in the mountains of Sonora near the United States border.

<sup>53</sup> See footnote 50.

- trast with the body blotches, not black; upper part of the proximal lobe of the rattle matrix only slightly, if at all, darkened.....*Crotalus scutulatus salvini*
- 32a. No paired dark vertebral stripes on the neck; or if present, not extending posteriorly as much as 1 head length before they meet the first dorsal blotches.....33
- 32b. On the neck a pair of quite regular dark stripes 1 to 3 scale rows wide, separated by a single light middorsal stripe 2 or 3 scale rows wide, these stripes extending from 1 to 4 head lengths behind the head before they meet the first dorsal blotches (fig. 2:143) . 37
- 33a. A black or dark-brown bar, bordered before and behind with cream or buff, crossing the head between the anterior points of the supraoculars. *Crotalus durissus totonacus* (fig. 2:23)
- 33b. No transverse bar in the prefrontal area as above described..... 34
- 34a. Tail usually black or very dark-brown with light crossbars seldom in evidence posteriorly; rattle matrix usually black.....*Crotalus molossus*  
(For subspecies continue on to 35)
- 34b. Tail usually gray, with light-gray crossbars in evidence posteriorly; rattle matrix usually gray or brown.....*Crotalus basiliscus*  
(For subspecies skip to 36)
- 35a. Scale rows at mid-body usually 27 or more; color of the internasal-prefrontal area darker than the posterior part of the head, which, however, is longitudinally streaked with lines of dark scales; light areas above the postocular dark stripes more than 2 scales wide; lateral interspaces nearer in color to the light rows of scales that bound the blotches, than to the dark colors of the blotch interiors.....*Crotalus molossus molossus* (fig. 2:43)
- 35b. Scale rows at mid-body usually 25 or fewer; color of the internasal-prefrontal area not conspicuously darker than the posterior part of the head, which, however, is longitudinally streaked with lines of light scales; light streaks 1 or 2 scales wide above the postocular dark stripes; lateral interspaces nearer in color to the dark areas of the dorsal blotches than to the light rows of scales that border these blotches.....*Crotalus molossus nigrescens* (fig. 2:45)
- 36a. Ventrals 177 or more in males; 184 or more in females; light and dark tail rings in moderate contrast.....*Crotalus basiliscus basiliscus* (fig. 2:13)
- 36b. Ventrals 176 or fewer in males; 183 or fewer in females; light and dark tail rings strongly contrasting.....*Crotalus basiliscus oaxacus* (fig. 2:14)
- 37a. The dark lines on the neck comprised more of single than of double or triple rows of dark scales; usually more than 4 scales in the internasal-prefrontal area  
*Crotalus durissus culminatus* (fig. 2:20)
- 37b. The dark lines on the neck comprised more of double (fig. 2:143) or triple rows of dark scales than of single; usually only 4 scales in the internasal-prefrontal area, comprising a pair of internasals and a pair of prefrontals or canthals (fig. 2:125) ..... 38
- 38a. Ventrals usually 179 or fewer in the males and 185 or fewer in the females; first infra-labials usually undivided (fig. 2:131) .....*Crotalus durissus durissus* (fig. 2:19)
- 38b. Ventrals usually 180 or more in the males and 186 or more in the females; first intra-labials usually divided transversely (fig. 2:132) ....*Crotalus durissus tzabcan* (fig. 2:24)
- 39a. Minimum intersupraoculars 4 or fewer.....*Crotalus lannomi*
- 39b. Minimum intersupraoculars 5 or more.....*Crotalus stejnegeri* (fig. 2:55)

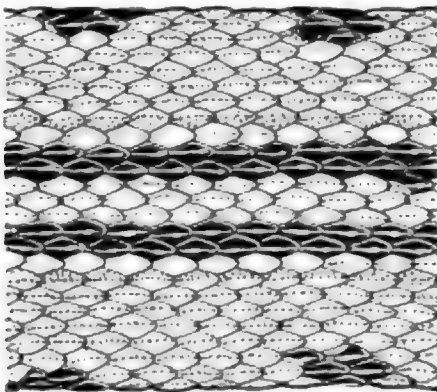


Fig. 2:143. Dorsal neck pattern of  
*C. d. durissus*

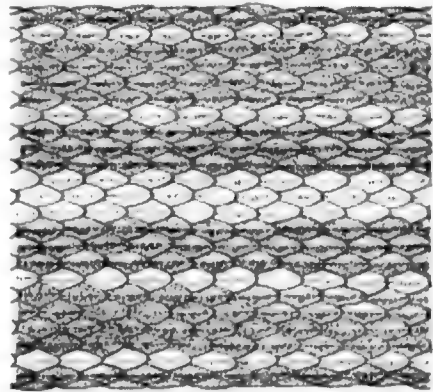


Fig. 2:144. Dorsal neck pattern of  
*C. d. terrificus*

KEY TO THE RATTLESNAKES OF  
BAJA (LOWER) CALIFORNIA, MEXICO

(Including the Islands of the Pacific Coast of the Peninsula,  
and of the Gulf of California)

- 1a. Rattle matrix shrunken; no loose rattle segment.....*Crotalus catalinensis* (fig. 2:15)
- 1b. Rattle matrix normal; almost always at least one or more loose rattle segments subsequent to the juvenile (button) stage.....2
- 2a. Outer edges of the supraoculars extended into pointed (but flexible) hornlike processes (figs. 2:104 and 2:105) .....*Crotalus cerastes laterorepens*<sup>51</sup> (fig. 2:18)
- 2b. Outer edges of the supraoculars not extended into pointed hornlike processes (figs. 2:106 and 2:107) ..... 3
- 3a. Prenasals usually separated from the rostral by small scales or granules, or at least the front edges of the prenasals chipped and sutured (fig. 2:113); upper preoculars often divided horizontally, vertically, or both (fig. 2:148) .....*Crotalus mitchellii*  
(For subspecies continue on to 4)
- 3b. Prenasals usually in contact with the rostral and without chipped or sutured front edges (fig. 2:107); upper preoculars rarely divided..... 7
- 4a. Last Supralabial about twice as long as those before it (fig. 2:148); head smaller, the length of the head contained in the adult body length (over-all) more than 24 times; original rattle-button, if present, more than 7½ mm. wide dorsoventrally  
*Crotalus mitchellii mitchellii* (fig. 2:38)
- 4b. Last supralabial not conspicuously longer than those before it; head larger, the length of the head contained in the adult body length (over-all) less than 24 times; original rattle-button, if present, less than 7½ mm. wide dorsoventrally..... 5
- 5a. Size smaller, adults seldom exceed 650 mm.; scale rows usually 23  
*Crotalus mitchellii muertensis* (fig. 2:40)
- 5b. Size larger, adults exceed 650 mm.; scale rows usually number 25 ..... 6
- 6a. Supraoculars without sutures or indentations at the outer edges; more than one scale between the prenasal and rostral.....*Crotalus mitchellii pyrrhus* (fig. 2:41)
- 6b. Supraoculars sutured, indented, or frayed at the outer edges; scale between the prenasal and rostral on each side as high as the prenasal. .*Crotalus mitchellii angelensis* (fig. 2:39)
- 7a. Usually 3 or more internasals (scales between the nasals and in contact with the rostral regardless of size or position, fig. 2:116) ..... 8

<sup>51</sup> The sidewinders of Tiburón Island are probably *C. c. cercobombus* rather than *C. c. laterorepens*, and I have so indicated in table 2:5. However, only a single specimen has been available from the island; until more is known concerning the sidewinders that occur there, I deem it inadvisable to include *cercobombus* in this key. If a distinction between *cercobombus* and *laterorepens* is required, see items 4a and 4b of the Mexican mainland key that precedes this one.

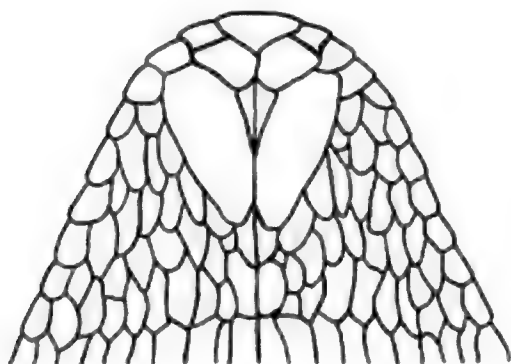


Fig. 2:145. Chin shields of *Crotalus*;  
intergenitals present.

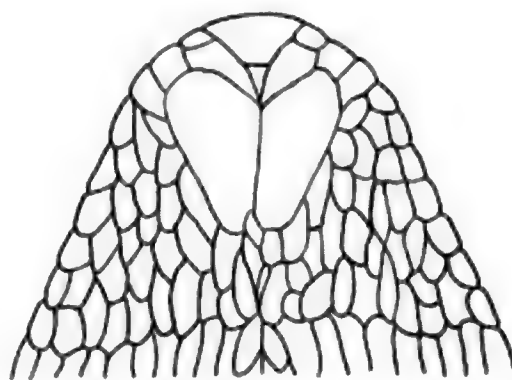


Fig. 2:146. Chin shields of *Crotalus*;  
submental present.

- 7b. Two internasals (fig. 2:117) ..... 9
- 8a. Adults smaller, rarely exceeding 650 mm..... *Crotalus viridis caliginis* (fig. 2:64)
- 8b. Adults larger, exceeding 650 mm..... *Crotalus viridis helleri* (fig. 2:67)
- 9a. Tail with alternating black and light ash-gray rings, both colors being in marked contrast with the posterior body color (fig. 2:126) ..... 10
- 9b. Tail not having alternating black and light ash-gray rings..... 14
- 10a. First infralabials usually divided (fig. 2:132); basic body color pink, red, or red-brown; dark punctations not conspicuous in dorsal blotches..... 11
- 10b. First infralabials usually undivided (fig. 2:131); basic body color cream, tan, buff, or gray; dorsal blotches conspicuously punctated with dark dots..... 13
- 11a. A pair of intergenials usually present (fig. 2:145); generally no contact between the prenasal and the first supralabial (fig. 2:121); dark tail rings often interrupted laterally.  
*Crotalus exsul* (fig. 2:29)
- 11b. Intergenials usually absent (fig. 2:132); prenasal usually contacts the first supralabial (fig. 2:123); dark tail rings rarely interrupted laterally..... *Crotalus ruber*  
(For subspecies continue on to 12)
- 12a. Usually a single loreal (fig. 2:123); scale rows usually 28 or more; light preocular stripe 2 scales wide or less (at the second row of scales above the supralabials); body color red or red-brown..... *Crotalus ruber ruber* (figs. 2:50 and 2:51)
- 12b. Usually 2 or more loreals (fig. 2:121); scale rows usually 27 or fewer; light preocular stripe 3 or more scales wide (at the second row of scales above the supralabials); body color yellow-brown or olive-brown..... *Crotalus ruber lucasensis* (fig. 2:52)
- 13a. Upper preocular usually in contact with the postnasal (fig. 2:122) or such contact prevented by an upper loreal (fig. 2:121) ..... *Crotalus atrox* (fig. 2:12)
- 13b. Upper preocular usually not in contact with the postnasal and no upper loreal present (fig. 2:123) ..... *Crotalus tortugensis* (fig. 2:57)
- 14a. Scales in the internasal and prefrontal areas total less than 12; scales on the crown and in the frontal area flat and smooth, although the edges may curl upward (fig. 2:125)  
*Crotalus molossus*  
(For subspecies continue on to 15)
- 14b. Scales in the internasal and prefrontal area total 12 or more; scales on the crown and in the frontal area rough, ridged, and knobby (fig. 2:147) ..... *Crotalus enyo*  
(For subspecies continue on to 16)
- 15a. Body blotches usually more than 37..... *Crotalus molossus estebanensis* (fig. 2:44)
- 15b. Body blotches usually fewer than 38..... *Crotalus molossus molossus* (fig. 2:43)
- 16a. Subcaudal scales usually more than 26 in males and more than 22 in females; adult head length contained in body length 26 times or more  
*Crotalus enyo cerralvensis* (fig. 2:26)
- 16b. Subcaudal scales usually 25 or fewer in males and 22 or fewer in females; adult head length contained in body length fewer than 26 times..... 17

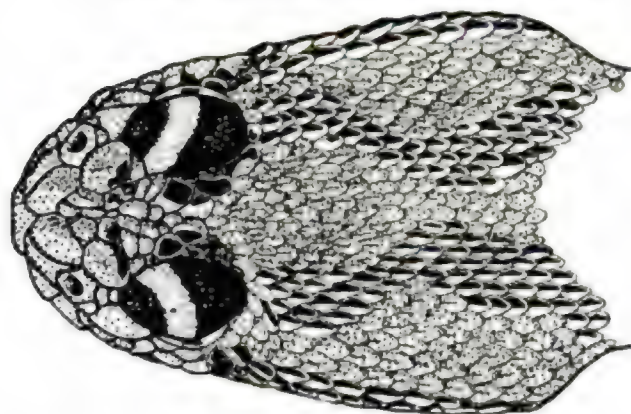


Fig. 2:147. Dorsal head pattern of *C. e. enyo*, showing light marks on supraoculars curving forward inwardly, and prefrontal and frontal scales rough and knobby.

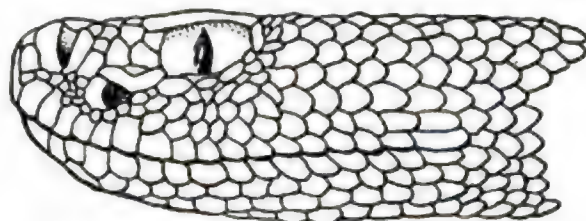


Fig. 2:148. *C. m. mitchellii* (lateral view), showing split upper preocular, foveals carried forward to the rostral, and last supra-labial twice as long as high.

- 17a. Ground color tan, fawn, or gray; upper loreal usually smaller than lower  
*Crotalus enyo enyo* (fig. 2:25)
- 17b. Ground color dark-brown; upper loreal usually larger than lower  
*Crotalus enyo fuvvus* (fig. 2:27)

# KEY TO THE RATTLESNAKES OF CENTRAL AND SOUTH AMERICA

- 1a. Clearly evident pattern comprising paravertebral stripes on the neck, followed by dorsal diamonds ..... 2
- 1b. Pattern not strongly evident (except in juveniles), not accentuated by contrasting light and dark colors ..... 4
- 2a. Light scale rows (one scale wide) laterally bounding the dark paravertebral stripes (or dorsal blotches) but little or no lighter than the lateral borders next below (fig. 2:143); dorsal diamonds darker and in strong contrast with the ground color of the sides. .... 3
- 2b. Light scale rows (one scale wide) laterally bounding the dark paravertebral stripes (or dorsal blotches) in strong color contrast with the next scales below on the sides (fig. 2:144); dorsal diamonds not in strong contrast with the lateral interdiamond areas  
*Crotalus durissus terrificus* (figs. 2:21 and 2:22)
- 3a. Ventrals usually 179 or fewer in the males and 185 or fewer in the females; first infralabials usually undivided (fig. 2:131) ..... *Crotalus durissus durissus* (fig. 2:19)
- 3b. Ventrals 180 or more in the males and 186 or more in the females; first infralabials usually divided transversely (fig. 2:132) ..... *Crotalus durissus tzabcan* (fig. 2:24)
- 4a. Pattern largely obliterated by scattered, white-tipped scales, dorsally and laterally  
*Crotalus vegrandis* (fig. 2:61)
- 4b. Pattern comprising paravertebral stripes on the neck and diamonds posteriorly, somewhat in evidence in yellowish-brown anteriorly and gray posteriorly, against a yellow or gray background. .... *Crotalus unicolor* (fig. 2:60)

# KEY TO THE GENERA OF THE CROTALIDAE BASED ON EXTERNAL CHARACTERS

(Devised by Bayard H. Brattstrom)<sup>55</sup>

- 1a. Rattles present. .... 2
- 1b. Rattles absent. .... 3
- 2a. Top of the head with large plates anteriorly (usually 9 in number) including a single frontal and a pair of large symmetrical parietals in contact (fig. 2:96). .... *Sistrurus*
- 2b. Top of the head with scales of varying sizes; more than one scale in the frontal area; parietals, if enlarged, neither in contact nor symmetrical (fig. 2:97) ..... *Crotalus*
- 3a. Top of head with large plates anteriorly (usually 9 in number) including a single frontal  
*Agkistrodon*
- 3b. Top of head with numerous small scales of varying sizes, including several or many scales in the frontal area. .... 4
- 4a. Posterior subcaudals in four rows. .... *Lachesis*
- 4b. Posterior subcaudals in one or two rows. .... 5
- 5a. A nasal pore present on the posterior wall of the nostril; smooth scales on top of the head anterior to the parietal region; Asiatic. .... *Trimeresurus*
- 5b. Nasal pore absent; all scales on top of the head usually keeled. .... 6
- 6a. Gular scales keeled; basic color green; Asiatic  
*Trimeresurus* (species *wagleri* and *philippensis*)
- 6b. Gular scales not keeled; basic color variable but usually brown with dark blotches; Mexican, and Central and South American. .... *Bothrops*

<sup>55</sup> For details of Brattstrom's work see Brattstrom 1964a, pp. 185-268

## KEY TO THE GENERA OF THE CROTALIDAE BASED ON THE ADULT SKULL

(Devised by Bayard H. Brattstrom)<sup>50</sup>

- 1a. Pterygoid teeth not extending posterior to the middle of the articulation of the ectopterygoid with the pterygoid..... 2
- 1b. Pterygoid teeth extending posterior to the middle of the articulation of the ectopterygoid with the pterygoid..... 4
  - 2a. Process at the border of the pit cavity of the maxillary with a well-developed cavity on its external surface..... *Lachesis*
  - 2b. Process at the border of the pit cavity of the maxillary even or smooth  
*Crotalus* and *Sistrurus* 3
- 3a. Lateral process of the squamosal forms a fork having an angle of 80° or less with the main bone  
*Sistrurus catenatus* and *Sistrurus miliarius*
- 3b. Lateral process of the squamosal blunt or pointed, but if it forms a fork with the main bone, then the angle between them is 90° or greater..... *Crotalus* and *Sistrurus ravus*
- 4a. Ectopterygoid shorter than the basal part of the pterygoid..... *Agkistrodon*
- 4b. Ectopterygoid longer than the basal part of the pterygoid..... 5
- 5a. Palatine in the form of a fork, with a dorsal process; anterior edge of the maxillary pit cavity has a smooth curve; Central and South American..... *Bothrops*
- 5b. Palatine not forked anteriorly; anterior edge of the maxillary pit cavity has a small process projecting toward the center of the pit; Asiatic..... *Trimeresurus*

## KEY TO THE SPECIES OF THE GENERA *CROTALUS* AND *SISTRURUS* BASED ON THE ADULT SKULL<sup>50</sup>

(Devised by Bayard H. Brattstrom)<sup>50</sup>

- 1a. Frontal square or wider than long..... 2
- 1b. Frontal (when measured at the middle) longer than wide..... 6
  - 2a. Frontal distinctly wider than long..... *C. adamanteus*
  - 2b. Frontal approximately square..... 3
- 3a. Articular with a thin ventrolateral process below the level of the junction with the quadrate..... 4
- 3b. Articular without such a process..... 5
  - 4a. Top of the parietal narrowing posteriorly; palatine teeth usually 2 (range 1-3); medial edge of the squamosal curved laterally..... *C. molossus*
  - 4b. Top of the parietal narrowing, followed by a rewidening within its anterior half; palatine teeth 3; medial edge of the squamosal usually straight..... *C. atrox*
- 5a. Palatine teeth usually 1 (range 0-2); top of the parietal elongate; ventral process of the basisphenoid has an anterior hump, when viewed from the side; middle and lower posterior processes of the prefrontal equal in length..... *C. durissus*
- 5b. Palatine teeth usually 3 (range 2-3); top of the parietal approximately square; ventral process of the basisphenoid without an anterior hump, when viewed from the side; lower posterior process of the prefrontal much shorter than the middle process..... *C. horridus*
  - 6a. No palatine teeth, and the dentary teeth fewer than 9..... 7
  - 6b. Palatine teeth present or absent, but, if absent, then the dentary teeth number more than 8..... 8
- 7a. Dentary teeth 8, pterygoid teeth 7..... *C. polystictus*

<sup>50</sup> Several species, including *C. transversus* and *C. unicolor*, are omitted for lack of adequate material. For the identification of the skull bones mentioned in this key, see figures 11:1 to 11:4.

- 7b. Dentary teeth 6 or 7, pterygoid teeth 4 or 5.....*C. stejnegeri*
- 8a. Squamosal long, narrow, thin, and with little or no lateral process; anterior end of the squamosal with small notches.....*C. pricei*
- 8b. Squamosal wide, flat, and relatively short; a lateral process present and usually well developed; anterior end of the squamosal rounded and even..... 9
- 9a. Lateral process of the squamosal forming a hook, thereby inclosing, or having an angle of 90° or less with, the main part of the squamosal.....10
- 9b. Lateral process of the squamosal forming an angle greater than 90° with the main part of the bone, or the process present only as a small knob.....18
- 10a. Top of the parietal rewidening in its anterior one-third, just behind the widening at the postfrontals.....*C. pusillus*
- 10b. Top of the parietal without rewidening, or if it does widen, then the second widest part is in its posterior two-thirds.....11
- 11a. Frontals slightly longer than wide, but appearing almost square; postfrontal touching the frontal; ventral process of the basisphenoid, when viewed from the side, has an anterior hump.....*C. basiliscus*
- 11b. Frontals much longer than wide; postfrontal not touching the frontal; ventral process of the basisphenoid, when viewed from the side, is without an anterior hump, or the entire ventral process is usually very low.....12
- 12a. Lateral hook of the squamosal makes an acute angle (45° to 80°) with the main part of the bone..... 13
- 12b. Lateral process of the squamosal substantially at right angles to the main part of the bone.....14
- 13a. Dentary teeth usually 10 (range 10–11); pterygoid teeth usually 8 (range 7–9); lower posterior process of the prefrontal longer than the middle process.....*S. miliarius*
- 13b. Dentary teeth usually 9 (range 9–10); pterygoid teeth usually 6 (range 5–7); lower posterior process of the prefrontal shorter than the middle process.....*S. catenatus*
- 14a. Frontal turned up laterally.....15
- 14b. Frontal flat.....16
- 15a. Squamosal long and narrow; top of the parietal substantially square; ventral process of the basisphenoid, when viewed from the side, with a slight anterior hump.....*C. willardi*
- 15b. Squamosal short and stubby; top of the parietal elongate; ventral process of the basisphenoid, when viewed from the side, low, without an anterior hump.....*C. lepidus*
- 16a. Medial edge of the pterygoid curved; nasals widest at the anterior end; palatine with a high dorsal hump and an elongate posterior extension.....*S. ravus*
- 16b. Medial edge of the pterygoid with an angle; nasals widest in the middle or posterior half; palatine low and stubby, with blunt anterior and posterior ends.....17
- 17a. Pterygoid teeth 5; articular foramen is posterior to the most anterior extension of the dorsal projection of the articular; angle of the medial edge of the pterygoid is in the posterior one-third of the bone; anterior border of the splenial at the anterior meckelian foramen curves forward or down.....*C. intermedius*
- 17b. Pterygoid teeth 6 or 7; articular foramen is anterior to the most anterior extension of the dorsal projection of the articular; angle of the medial edge of the pterygoid is in the middle one-third of the bone; anterior border of the splenial at the anterior meckelian foramen curves backward.....*C. triseriatus*
- 18a. Ventral curvature of the loreal-pit cavity in the maxilla with only a shallow depression, or with an indentation only at right angles to the curvature; ventral process of the basisphenoid well developed.....19
- 18b. Ventral curvature of the loreal-pit cavity in the maxilla with a deep, forward-directed, indentation; ventral process of the basisphenoid usually not well developed.....23
- 19a. Frontals considerably longer than wide; upper posterior process of the prefrontal longer than the lower.....*C. enyo*
- 19b. Frontals slightly longer than wide, almost square; lower posterior process of the prefrontal longer than the upper.....20
- 20a. Postfrontal separated from the frontal; lateral process of the squamosal pointed; lateral process at the anterior end of the ectopterygoid wide and with a slight downward bend  
*C. tortugensis*

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- 20b. Postfrontal in contact with the frontal or separated by less than  $\frac{1}{4}$  mm.; lateral process of the squamosal usually blunt; lateral process at the anterior end of the ectopterygoid rounded.....21
- 21a. Top of the parietal narrowing posteriorly with no rewidening; ventral process of the basisphenoid rectangular when viewed from the side.....*C. ruber* and *C. exsul*
- 21b. Top of the parietal rewidening in its posterior two-thirds; ventral process of the basisphenoid triangular when viewed from the side.....22
- 22a. Top of the parietal rewidening in its anterior half.....*C. horridus*
- 22b. Top of the parietal rewidening in its posterior half.....*C. atrox*
- 23a. Ventral process of the basisphenoid very slightly developed; frontal distinctly turned up laterally.....*C. cerastes*
- 23b. Ventral process of the basisphenoid somewhat developed (usually more than  $\frac{1}{4}$  mm.); frontal flat or only slightly turned up laterally.....24
- 24a. Area between the processes at the anterior end of the ectopterygoid curved; posterior part of the pterygoid short, stubby, wide, and with the medial edge curved....*C. tigris*
- 24b. Area between the processes at the anterior end of the ectopterygoid flat; posterior part of the pterygoid elongate and relatively narrow; medial edge of the pterygoid with an angle, occasionally curved.....25
- 25a. Lower posterior process of the prefrontal wide and longer than the middle process  
*C. scutulatus*
- 25b. Middle posterior process of the prefrontal longer than the lower process, the latter often short and stubby.....26
- 26a. Palatine with a definite anterior knob; anterior edge of the transverse bar of the premaxilla, when seen from above, coming to a point; top of the parietal narrowing posteriorly.....*C. viridis*
- 26b. Palatine usually without an anterior knob; anterior edge of the transverse bar of the premaxilla, when seen from above, curved or rounded; top of the parietal rewidening in its posterior one-third.....*C. mitchellii*

TABLES OF GEOGRAPHICAL DISTRIBUTION

In the geographical tables that follow, it should be observed that the numbers in parentheses apply to specific numbered notes appended to each table individually. The following letters and other symbols are applicable to all tables:

+	Present in the area	Nw	Northwest
C	Central area	P	Probably present, but no definite record
E	East	S	South
Ec	East-central	Sc	South-central
Ex	Extreme (example, ExS is extreme south)	Se	Southeast
N	North	Sw	Southwest
Nc	North-central	W	West
Ne	Northeast	Wc	West-central

A comma stands for "and"; thus C,E means the central and eastern parts of the area.

TABLE 2:1

GEOGRAPHICAL DISTRIBUTION OF RATTLESNAKES IN CANADA

Province	<i>S. c. calenatus</i>	<i>C. A. horridus</i>	<i>C. v. viridis</i>	<i>C. v. oregonus</i>
Alberta.....	....	....	(3)	....
British Columbia.....	....	....	....	(5)
Ontario.....	(1)	(2)	....	....
Saskatchewan.....	....	....	(4)	....

- (1). Southern Ontario along the shores of Georgian Bay, Lake Huron, and Lake Erie; also Prince Edward Peninsula in Lake Ontario.
- (2). Vicinity of Niagara Glen; it once occurred at several points on the north shore of Lake Erie, but probably has now been exterminated there, except possibly at Point Pelee, Essex County.
- (3). Southeastern Alberta, from the Red River south to the border.
- (4). Southwestern Saskatchewan from the South Saskatchewan River south to the border.
- (5). South-central British Columbia within the triangle Lillooet-Shuswap Lake-Osoyoos; also east along the United States border to Christina Lake, and possibly to Waneta.

TABLE 2:2

GEOGRAPHICAL DISTRIBUTION OF RATTLESNAKES IN THE UNITED STATES  
EAST OF THE MISSISSIPPI RIVER

State	<i>S. c. calenatus</i>	<i>S. m. miliarius</i>	<i>S. m. barbouri</i>	<i>S. m. streckeri</i>	<i>C. ada- mantus</i>	<i>C. A. horridus</i>	<i>C. A. atri- caudatus</i>
Alabama.....	..	C	S	P(Nw)	S	N	C,S
Connecticut.....	..	..	..	..	..	+	..
Delaware.....	..	..	..	..	..	(2)	..
District of Columbia.....	..	..	..	..	..	(3)	..
Florida.....	..	..	+	..	+	..	N,W
Georgia.....	..	C	S	..	S	N	C,S
Illinois.....	+	..	..	..	..	S,W	ExS
Indiana.....	C,N	..	..	..	..	S	..
Kentucky.....	..	..	..	S,W	..	+	ExW
Louisiana.....	..	..	..	+	E	..	+
Maine.....	..	..	..	..	..	(4)	..
Maryland.....	..	..	..	..	..	N,W	..
Massachusetts.....	..	..	..	..	..	+	..
Michigan.....	(1)	..	..	..	..	..	..
Mississippi.....	..	..	Se	+	S	..	+
New Hampshire.....	..	..	..	..	..	C,Sw	..
New Jersey.....	..	..	..	..	..	+	..
New York.....	Nw	..	..	..	..	+	..
North Carolina.....	..	Se	..	..	E	W	E
Ohio.....	C,N	..	..	..	..	S	..
Pennsylvania.....	ExW	..	..	..	..	+	..
Rhode Island.....	..	..	..	..	..	+	..
South Carolina.....	..	+	ExS	..	Se	Nw	C,Se
Tennessee.....	..	..	..	Sw	..	C,E	W
Vermont.....	..	..	..	..	..	S	..
Virginia.....	..	..	..	..	..	W	ExSe
West Virginia.....	..	..	..	..	..	+	..
Wisconsin.....	Sw	..	..	..	..	Sw	..

- (1). *S. c. calenatus* is generally distributed in Lower, but has not been reported in Upper Michigan.
- (2). Rattlesnakes have apparently been exterminated in the Del-Mar-Va Peninsula, if indeed they ever occurred there. No authentic records of *C. A. horridus* from Delaware in historic times are at hand.
- (3). Although *C. A. horridus* once occurred in the District of Columbia, it seems now to have been exterminated. An occasional specimen may still be carried in by a river flood.
- (4). Although once present in southwestern Maine, *C. A. horridus* seems to have been exterminated there, probably some- time prior to 1860 (see Palmer, 1946, p. 1). In 1946 I addressed inquiries to a number of game wardens in the area in Maine where the remnants of any colony might be expected to remain. None reported any recent evidences of rattle- snakes. Maine and Delaware are apparently today the only states in which rattlesnakes are no longer found, although there are large areas within other states—Minnesota and Wisconsin particularly—where no rattlers occur.

TABLE 2:5  
GEOGRAPHICAL DISTRIBUTION OF THE RATTLESNAKES OF BAJA CALIFORNIA, MEXICO, AND THE ADJACENT ISLANDS

Area	<i>C. atrox</i>	<i>C. catalinensis</i>	<i>C. c. cercoombus</i>	<i>C. c. laterorepens</i>	<i>C. e. enyo</i>	<i>C. e. cervicalensis</i>	<i>C. e. furvus</i>	<i>C. ezul</i>	<i>C. m. mitchellii</i>	<i>C. m. angelensis</i>	<i>C. m. muertensis</i>	<i>C. m. pyrrhus</i>	<i>C. m. molossus</i>	<i>C. m. calcebanensis</i>	<i>C. r. ruber</i>	<i>C. r. lucasensis</i>	<i>C. tortugensis</i>	<i>C. v. caliginis</i>	<i>C. v. helleri</i>
	Ne	:	:	Ne	C,S	:	Nw	:	S	:	:	N,C	:	:	N,C	S	:	:	Nw,C
Peninsula of Baja California.....	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Islands:	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Los Coronados.....	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cedros.....	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Magdalena.....	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Santa Margarita.....	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cerralvo.....	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Espíritu Santo.....	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Isla Partida (South).	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
San Francisco.....	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
San José.....	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Santa Cruz.....	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Santa Catalina.....	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Monserate.....	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Carmen.....	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
San Marcos.....	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Tortuga.....	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
San Pedro Mártir...	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
South San Lorenzo..	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
San Esteban.....	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Turner.....	++	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Tiburón.....	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Pond.....	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Ángel de la Guarda..	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Smith.....	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
El Muerto.....	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

TABLE 2:6  
GEOGRAPHICAL DISTRIBUTION OF RATTLESNAKES IN CENTRAL AND SOUTH AMERICA

Country	<i>C. d. durissus</i>	<i>C. d. terrificus</i>	<i>C. d. tzabcan</i>	<i>C. unicolor</i>	<i>C. vegrandis</i>
Central America:					
British Honduras.....	+(1)	..	N(1)	..	..
Guatemala.....	+(1)	..	N(1)	..	..
El Salvador.....	+	..	..	..	..
Honduras.....	W,C	..	..	..	..
Nicaragua.....	W	..	..	..	..
Costa Rica.....	Nw	..	..	..	..
Panama.....	(2)	..	..	..	..
Canal Zone.....	..	..	..	..	..
South America:					
Colombia.....	..	N,C	..	..	..
Venezuela.....	..	+	..	..	ExNe
Guyana (formerly British Guiana).....	..	+	..	..	..
Surinam.....	..	+	..	..	..
French Guiana.....	..	+	..	..	..
Brazil.....	..	+	..	..	..
Ecuador.....	..	(3)	..	..	..
Peru.....	..	ExSe	..	..	..
Bolivia.....	..	+	..	..	..
Paraguay.....	..	+	..	..	..
Uruguay.....	..	+	..	..	..
Argentina.....	..	N,C	..	..	..
Chile.....	..	..	..	..	..
Aruba Island (off Vene- zuela).....	..	..	..	+	..

(1). The boundary between *C. d. durissus* and *C. d. tzabcan* in northern Guatemala and in British Honduras is not known with accuracy.  
(2). Although there have been reports of rattlesnakes in Panama, none has been verified by an identified specimen.  
(3). General statements have been made to the effect that *C. d. terrificus* occurs in eastern Ecuador, but no authentic records are available. Little is known concerning the presence of rattlesnakes in the western part of the Amazon basin.

## TABLES OF CHARACTER VARIATIONS

The numbers in parentheses in tables 2:7 and 2:8 represent the means of the items listed, except for the scale rows at mid-body, in which the mode is indicated. The body blotches are counted only to the base of the tail, any tail marks being omitted from the count. I have not listed the tail rings, because in many species they cannot be counted with accuracy; they are seldom of use in discriminating between forms, except in the subspecies of *C. viridis*.<sup>57</sup>

With regard to the statistics of squamation in table 2:7, it should be stated that there were insufficient specimens of the following species and subspecies to determine the ranges of variation and averages with any degree of finality: *C. enyocerraleensis*, *C. enyo furvus*, *C. intermedius intermedius*, *C. lannomi*, *C. pricei miquihuanus*, *C. pusillus* (females), *C. scutulatus salvini*, *C. stejnegeri*, *C. transversus*, and *C. willardi meridionalis*.

The range in the ventrals in *C. triseriatus triseriatus* does not include the type specimen with 159. In several places I have not hesitated to omit scale counts so different from the normal as to be clearly from freaks, or possibly from miscounts that could not be verified because the specimens were no longer available.

The statistics of teeth presented in table 2:8 represent the researches of Bayard H. Brattstrom.

<sup>57</sup> The statistics of the tail rings of the *viridis* subspecies are as follows (the first pair of figures under each subspecies is the range in the males, followed by the mean in parentheses, after which the same data on the females are given): *viridis* 6-15 (9.9), 4-11 (7.4); *abyssus* 7-12 (8.2), 6-8 (6.9); *caliginis* 4-6 (5.2), 3-5 (4.2); *cerberus* 3-9 (6.1), 3-7 (4.6); *concolor* 7-11 (R.GQ, F-VJ) (7.2); *helleri* 3-8 (4.5), 2-6 (3.4); *lutosus* 5-10 (7.1), 4-8 (5.6); *nuntius* 5-12 (9.4), 5-10 (7.1); *oreganus* 3-10 (5.6), 3-8 (4.5).

TABLE 2:8  
TEETH SOCKET COUNTS  
(Range of variation, followed by mean in parentheses)  
(Data prepared by B. H. Brattstrom, 1964a, pp. 194, 196)

Species	Specimens examined	Palatine	Pterygoid	Dentary
<i>C. adamanteus</i> .....	39, 40, 39 <sup>1</sup>	1-3 (2.7)	7-11 (8.1)	9-10 (9.5)
<i>C. atrox</i> .....	67, 70, 70	3 (3.0)	7-9 (8.0)	7-11 (9.9)
<i>C. basiliscus</i> .....	4, 4, 4	0-2 (1.0)	7-8 (7.5)	9-11 (9.8)
<i>C. cerastes</i> .....	44, 46, 45	2-4 (3.0)	7-9 (8.4)	8-11 (9.8)
<i>C. durissus</i> .....	18, 12, 14	0-2 (1.1)	7-9 (7.8)	8-11 (9.8)
<i>C. enyo</i> .....	6, 2, 4	1-3 (2.7)	8 (8.0)	9-11 (10.0)
<i>C. horridus</i> .....	28, 34, 34	2-3 (2.9)	8-11 (8.7)	10-13 (10.9)
<i>C. intermedius</i> .....	1, 1, 1	3 (3.0)	5 (5.0)	8 (8.0)
<i>C. lepidus</i> .....	7, 8, 10	2-3 (2.7)	6-8 (6.9)	8-9 (8.1)
<i>C. mitchellii</i> .....	15, 24, 23	2-3 (2.9)	7-10 (8.2)	7-10 (8.9)
<i>C. molossus</i> .....	12, 12, 9	1-3 (2.1)	6-10 (8.8)	9-11 (10.0)
<i>C. polystictus</i> .....	2, 2, 2	0 (0.0)	7 (7.0)	8 (8.0)
<i>C. pusillus</i> .....	9, 9, 10	3 (3.0)	7-9 (7.7)	9-11 (10.1)
<i>C. pricei</i> .....	3, 5, 3	3 (3.0)	6-7 (6.6)	9-10 (9.3)
<i>C. ruber</i> .....	27, 26, 31	3 (3.0)	6-9 (8.0)	8-11 (9.5)
<i>C. scutulatus</i> .....	16, 16, 14	3 (3.0)	6-8 (7.3)	9-10 (9.6)
<i>C. stejnegeri</i> .....	4, 3, 4	0 (0.0)	4-5 (4.7)	6-7 (6.5)
<i>C. tigris</i> .....	4, 4, 3	3 (3.0)	7-9 (8.0)	9-10 (9.3)
<i>C. tortugensis</i> .....	2, 2, 2	3 (3.0)	9 (9.0)	10 (10.0)
<i>C. triseriatus</i> .....	4, 5, 3	3 (3.0)	6-7 (6.2)	7-8 (7.3)
<i>C. viridis</i> .....	103, 108, 107	2-4 (2.9)	6-10 (7.4)	6-11 (9.3)
<i>concolor</i> .....	1, 2, 2	3 (3.0)	6-7 (6.5)	9 (9.0)
<i>lutosus</i> .....	8, 6, 6	2-3 (2.5)	7-8 (7.2)	9-10 (9.3)
<i>helleri</i> .....	47, 52, 50	3 (3.0)	7-10 (7.8)	8-11 (9.4)
<i>oreganus</i> .....	17, 16, 18	2-4 (3.1)	6-9 (7.8)	9-10 (9.6)
<i>viridis</i> .....	30, 32, 31	2-3 (3.0)	7-9 (7.7)	6-11 (9.1)
<i>C. willardi</i> .....	4, 6, 5	1-2 (1.8)	5-7 (6.2)	8 (8.0)
<i>S. catenatus</i> .....	17, 19, 20	1-3 (2.6)	5-7 (5.6)	9-10 (9.1)
<i>S. miliarius</i> .....	2, 4, 7	3 (3.0)	7-9 (7.8)	10-11 (10.4)
<i>S. ravus</i> .....	10, 10, 10	3 (3.0)	5-7 (5.9)	8-10 (8.8)

<sup>1</sup> Available counts listed in the order: palatine, pterygoid, dentary. For positions of these teeth, see figures 11:1 to 11:4.

TABLE 2:9  
TABULAR INDEX TO CHAPTER 2

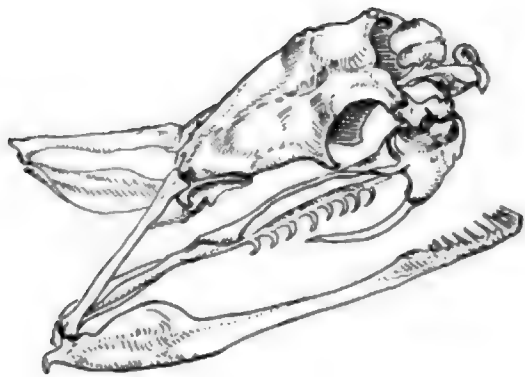
Species or subspecies	Range, page	Map		Photograph	
		page	figure <sup>a</sup>	page	figure <sup>a</sup>
<i>C. adamanteus</i> .....	31	58	1	65	11
<i>C. atrox</i> .....	32	58	1	65	12
<i>C. basiliscus basiliscus</i> .....	32	59	2	66	13
<i>oaxacus</i> .....	32	59	2	66	14
<i>C. catalinensis</i> .....	33	63	9	67	15
<i>C. cerastes cerastes</i> .....	33	59	3	67	16
<i>cercobombus</i> .....	33	59	3	68	17
<i>laterorepens</i> .....	34	59	3	68	18
<i>C. durissus durissus</i> .....	34	60	4	69	19
<i>culminatus</i> .....	34	60	4	69	20
<i>terrificus</i> .....	35	60	5	70	21, 22
<i>tolonacus</i> .....	37	60	4	71	23
<i>tzabcan</i> .....	37	60	4	71	24
<i>C. enyo enyo</i> .....	37	59	3	72	25
<i>cerralvensis</i> .....	37	59	3	72	26
<i>furvus</i> .....	38	59	3	73	27, 28
<i>C. exsul</i> .....	38	58	1	74	29
<i>C. horridus horridus</i> .....	38	61	6	74	30
<i>atricaudatus</i> .....	39	61	6	75	31
<i>C. intermedius intermedius</i> .....	39	63	8	76	32
<i>gloydi</i> .....	40	63	8	76	33
<i>omiltemanus</i> .....	40	63	8	76	34
<i>C. lannomi</i> .....	40	64	10	..	..
<i>C. lepidus lepidus</i> .....	41	62	7	77	35
<i>klauberi</i> .....	41	62	7	77	36, 37
<i>morulus</i> .....	41	62	7	..	..
<i>C. mitchellii mitchellii</i> .....	42	62	7	78	38
<i>angelensis</i> .....	42	62	7	79	39
<i>muertensis</i> .....	42	62	7	79	40
<i>pyrrhus</i> .....	43	62	7	80	41
<i>stephensi</i> .....	43	62	7	80	42
<i>C. molossus molossus</i> .....	43	59	2	81	43
<i>estebanensis</i> .....	44	59	2	81	44
<i>nigrescens</i> .....	44	59	2	82	45
<i>C. polystictus</i> .....	44	63	8	..	..
<i>C. pricei pricei</i> .....	45	63	8	82, 83	46, 47
<i>miquihuanus</i> .....	45	63	8	83	48
<i>C. pusillus</i> .....	46	64	10	84	49
<i>C. ruber ruber</i> .....	46	58	1	84, 85	50, 51
<i>lucasensis</i> .....	46	58	1	85	52
<i>C. scutulatus scutulatus</i> .....	47	63	9	86	53, 54
<i>salvini</i> .....	47	63	9	..	..
<i>C. stejnegeri</i> .....	47	64	10	87	55
<i>C. tigris</i> .....	48	62	7	87	56
<i>C. tortugensis</i> .....	48	58	1	88	57
<i>C. transversus</i> .....	48	63	8	..	..
<i>C. triseriatus triseriatus</i> .....	48	62	7	88	58
<i>aquilus</i> .....	49	62	7	89	59
<i>C. unicolor</i> .....	49	60	5	89	60

<sup>a</sup> The chapter prefix number is omitted; that is, figure 2:14 is tabulated as 14.

TABLE 2:9—Continued

Species or subspecies	Range, page	Map		Photograph	
		page	figure <sup>a</sup>	page	figure <sup>a</sup>
<i>C. vegrandis</i> .....	49	60	5	90	61
<i>C. viridis viridis</i> .....	50	61	6	90	62
<i>abyssus</i> .....	50	61	6	91	63
<i>caliginis</i> .....	51	61	6	91	64
<i>cerberus</i> .....	51	61	6	92	65
<i>concolor</i> .....	51	61	6	92	66
<i>helleri</i> .....	52	61	6	93	67
<i>lutosus</i> .....	52	61	6	93	68
<i>nuntius</i> .....	52	61	6	94	69
<i>oreganus</i> .....	53	61	6	94, 95	70, 71
<i>C. willardi willardi</i> .....	54	59	3	95	72
<i>amabilis</i> .....	54	59	3	96	73
<i>meridionalis</i> .....	54	59	3	96	74
<i>silus</i> .....	54	59	3	97	75
<i>S. catenatus catenatus</i> .....	55	64	10	97	76
<i>edwardsii</i> .....	55	64	10	98	77
<i>tergeminus</i> .....	56	64	10	98	78
<i>S. miliarius miliarius</i> .....	56	64	10	99	79
<i>barbouri</i> .....	56	64	10	99	80
<i>streckeri</i> .....	57	64	10	100	81
<i>S. ravidus</i> .....	57	64	10	100	82

Some tables, in this and other chapters, wherein various characters are enumerated by species and subspecies are the following: *squamation and blotches*, table 2:7, following p. 142; *teeth sockets*, table 2:8, p. 143; *lengths*, table 4:1, p. 175; *head proportions*, table 4:2, p. 136; *tail proportions*, table 4:3, p. 190; *rattle dimensions*, table 5:6, p. 321; *hemipenial characters*, table 10:2, p. 698; *brood sizes*, table 10:3, p. 733; *fang proportions*, table 11:1, p. 768; and *venom yields*, tables 11:7–11:8, pp. 808–810.



### 3. Paleontology, Zoögeography, and Phylogeny

#### PALEONTOLOGY

Less is known about fossil snakes than about any other vertebrate group. Their small size and delicate bones have resulted in a meager record. Most of the characters used in the classification of existent snakes, particularly the scales, are not preserved as fossils; this renders correlation with the classification of living species difficult. Rattles do not fossilize. The taxonomic and phylogenetic studies of snakes, particularly at the species level, are thus little aided by paleontology, and are more completely dependent on living forms than is the case with other suborders. But some fossil rattlesnake remains are available for study.

#### ANTIQUITY OF SNAKES

Snakes seem to have originated rather late in the Age of Reptiles. Bellairs and Underwood (1951, p. 195) place the oldest fossil snakes in the Lower Cretaceous of central Europe. A few ophidian vertebrae are known from the Upper Cretaceous of the Old World, and Upper Cretaceous remains have been found in Patagonia. The major evolution of the snakes, with the gradual development of a perfected venom apparatus in some families, must have occurred during the four successive divisions of the Tertiary—the Eocene, Oligocene, Miocene, and Pliocene—with proliferation in the lately past Pleistocene (the Ice Age), continuing into the contemporary or Recent, the latter name being given to our present time zone or period as a component of the geological series.

According to Gilmore (1938, p. 70) venomous snakes made their first appearance in Europe in the Miocene age. Romer (1945, p. 208; 1956, p. 568) stated that snakes are the newest of the reptilian groups, first appearing in the late Cretaceous and Eocene. It was his opinion that poisonous snakes, with grooved or hollow fangs, were evolved later; they are not surely known before the Miocene.

The most ancient specimens definitely to be considered rattlesnake fossils are from Driftwood Creek, Hitchcock County, Nebraska, probably of Lower Pliocene age, but possibly Upper Miocene. A guess at their age might be anywhere from 4 to 12 million years (Gilmore, 1938, p. 72; Brattstrom, 1954b, p. 33; Fitch, 1960, p. 115; Gehlbach, 1965, p. 61). Auffenberg (1963, p. 134) mentions Pliocene remains from near Haile, Alachua County, Florida, which may belong to the Crotalidae, and might, therefore, be the vestiges of a rattlesnake.

## RATTLESNAKE FOSSILS

Fossil remains of rattlesnakes, usually vertebrae, with occasional ribs, fangs, and skull bones, are moderately common in paleontological collections. They have been found in caves, lime pits, and similar excavations, and in the asphalt pits of California. Most of them are known to be from the Pleistocene, but a few may be from Pliocene horizons. The localities where these fossil rattlesnake remains have been discovered and the nature of the material itself are described in the following references: Wheatley (1871, p. 235), Hay (1902a, p. 481; 1917, p. 44; 1920, pp. 96, 135; 1923, pp. 314, 348, 353, 382; 1924, pp. 147, 251; 1927, p. 216; 1929, vol. 2, p. 271), Sinclair (1904, pp. 11, 18, 19), Barnum Brown (1908, p. 207), L. H. Miller (1912, p. 71), Stock (1918, p. 461), Gridley (in Hay, 1927, p. 216), Merriam (in Bryant, 1929, p. 48), Harrington (1933, p. 192), Gilmore (1938, p. 70), Brattstrom (1953a, p. 367; 1953b, p. 174; 1953c, p. 243; 1954a, p. 8; 1951b, p. 31; 1955a, p. 153; 1955b, p. 4; 1958, pp. 8, 12; 1964a, p. 185; 1964b, p. 93), Van Frank and Hecht (1954, p. 158), Dowling (1958, p. 6), Holman (1958, p. 278; 1959a, p. 100; 1959b, p. 124; 1963, p. 152; 1964, p. 82), Mecham (1959, p. 25), Auffenberg (1963, p. 134), Guilday, Martin, and McCrady (1964, p. 142), Gut and Ray (1964, p. 320), and Gehlbach (1965, p. 61).

## CLASSIFICATION OF FOSSILS

Gilmore (1938, p. 72) was unable to differentiate such modern species as *horridus*, *confluentus* (= *viridis*), *adamanteus*, and *atrox* on vertebral characters—the only evidence usually remaining—and thought that it was therefore impossible to go beyond the statement that the animal represented was probably a rattlesnake. It might even be that some of these remains represented pit vipers other than rattlesnakes. From the size of some of the fossil remains and their location in Florida, it could be assumed that they were those of the eastern diamondback (*C. adamanteus*), but of this there was no certainty. Therefore, Gilmore did not follow the earlier authors (Hay especially) in assigning the fossils to the existent species now present in the areas where the remains were found, but, except in the case of *adamanteus*, merely considered them to belong to the rattlesnake genus *Crotalus*.

More recently, B. H. Brattstrom (1953b, 1954b, 1964a) has made a complete study of the fossil crotalid remains available in this country, including osteological comparisons with existing species. He has not only been able to make generic segregations with certainty, but likewise some specific distinctions, based on vertebrae and skulls. The works of Holman (1958, 1959a, 1959b, 1963, 1964) and Auffenberg (1963) have also been important in the allocation of rattlesnake fossil remains.

The characteristic features of a rattlesnake vertebra are shown in figures 3:1 to 3:3. The proportions of the mid-thoracic vertebrae of typical species and subspecies are presented in table 3:1. In addition, data on the numbers of teeth in the several series have been set forth in table 2:9. The application of differential cranial characteristics to the segregation, first of the genera of the crotalids, and secondly of the species within the rattlesnake genera *Sistrurus* and *Crotalus*, has been indicated in two of the keys in chapter 2 (p. 136). The illustrations in which the skull parts are named will be found in chapter 11 (figs. 11:1–11:4).

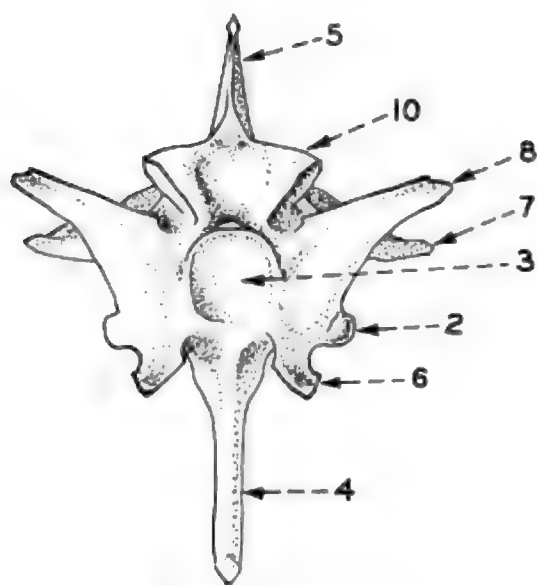


Fig. 3:1. Front view.

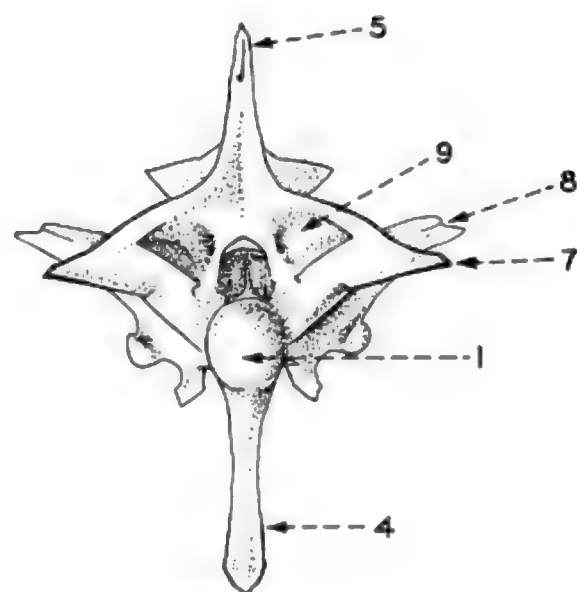


Fig. 3:2. Rear view.

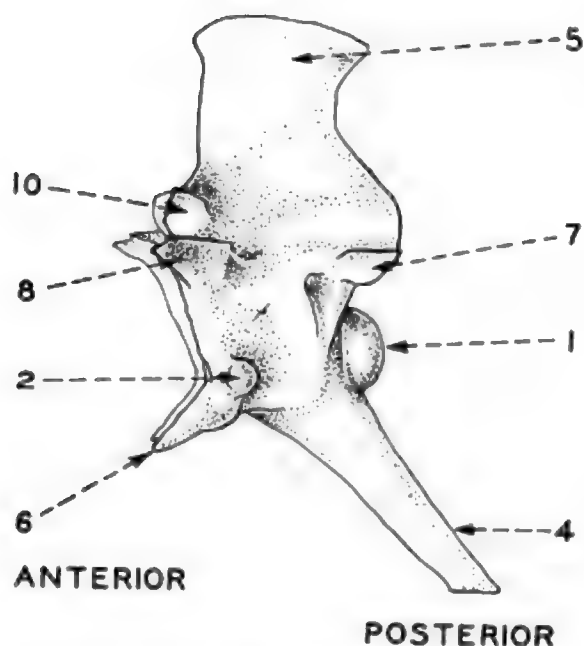


Fig. 3:3. Side view (drawings by Mrs. Joan Arsenault, prepared under the direction of B. H. Brattstrom.)

Mid-thoracic vertebra of *Crotalus ruber ruber*

- 1. Condyle or ball of centrum
- 2. Diapophysis (transverse process)
- 3. Glenoid cavity or cup of centrum
- 4. Hypapophysis
- 5. Neural spine
- 6. Parapophysis
- 7. Postzygapophysis
- 8. Prezygapophysis
- 9. Zygantrum
- 10. Zygosphene

TABLE 3:1  
PROPORTIONS OF MID-THORACIC VERTEBRAE IN ADULT RATTLESNAKES AND MOCCASINS  
(Based on Brattstrom, 1964a, p. 209, table 8)

Species or subspecies	Ratio of height to width <sup>a</sup>	Ratio of height of neural spine to height over-all	Ratio of neural spine to width
<i>C. adamanteus</i> .....	1.52	0.36	0.55
<i>C. atrox</i> .....	1.60	0.37	0.59
<i>C. basiliscus</i> .....	1.61	0.27	0.43
<i>C. cerastes</i> .....	1.31	0.35	0.46
<i>C. d. tzabcan</i> .....	1.72	0.41	0.71
<i>C. enyo</i> .....	1.78	0.44	0.79
<i>C. lepidus</i> .....	1.79	0.33	0.42
<i>C. mitchellii</i> .....	1.03	0.41	0.42
<i>C. molossus</i> .....	.....	.....	0.45
<i>C. pricei</i> .....	1.29	0.25	0.33
<i>C. ruber</i> .....	1.34	0.33	0.45
<i>C. scutulatus</i> .....	1.43	0.32	0.46
<i>C. tigris</i> .....	1.67	0.36	0.60
<i>C. v. viridis</i> .....	1.21	0.29	0.34
<i>C. v. concolor</i> .....	1.19	0.30	0.35
<i>C. willardi</i> .....	0.97	0.27	0.27
<i>S. catenatus</i> .....	1.53	0.34	0.52
<i>S. miliarius</i> .....	1.41	0.26	0.37
<i>A. contortrix</i> .....	1.57	0.34	0.54
<i>A. piscivorus</i> .....	1.51	0.43	0.65

<sup>a</sup> The height is measured from the tip of the neural spine to the end of the hypapophysis; the width is measured across the postsygapophyses.

EXTINCT RATTLESNAKES

Brattstrom has described two species and one subspecies of rattlesnakes now extinct. These are:

1953. *Crotalus potterensis* Brattstrom, Copeia, No. 3, p. 173. Type locality, Potter Creek Cave, Shasta County, California. Late Pleistocene. Most closely related to *C. viridis*, from which it differs in the size and shape of the vertebrae and in having a pterygoid larger than that of existent *viridis*.
1954. *Crotalus adamanteus pleistofloridensis* Brattstrom, Trans. San Diego Soc. Nat. Hist., vol. 12, no. 3, p. 35. Type locality, Seminole, Pinellas County, Florida. Late Pleistocene. Differs from existent *C. adamanteus* in being larger (twice as large in bulk), with a higher neural spine and other differences in the shape of the vertebrae. Since the original description, additional material, said by Brattstrom (1954b, p. 40) to represent this subspecies, has been found at Allen Cave, Lecanto, Citrus County; Melbourne, Brevard County; and Vero Beach, Saint Lucie County. All are Florida Pleistocene deposits.
1954. *Crotalus giganteus* Brattstrom, Trans. San Diego Soc. Nat. Hist., vol. 12, no. 3, p. 36. Type locality, Allen Cave, Lecanto, Citrus County, Florida. Pleistocene. Differs from existent *C. adamanteus* in being markedly larger, reaching a body length in life of possibly 12 feet. The vertebrae also differ somewhat in shape from those of *adamanteus*. Since the original description of *C. giganteus* additional fossil remains (either Pleistocene and/or Recent) have been found at the following Florida localities: Haile VII (Limestone Quarry), and Hornsby Springs, Alachua County; Eichelberger Cave, Marion County; and Rock Springs, Orange County.

Dowling (1958, p. 6) and Auffenberg (1963, p. 204) consider *C. a. pleistofloridensis* insufficiently differentiated from *C. adamanteus* to be recognized as a valid subspecies. Auffenberg (1963, p. 205) believes *giganteus* also of questionable status.

## LOCALITIES AND AGE OF FOSSILS

Brattstrom, especially in his 1954b and 1964a publications, has been able to point out previously unrecognized generic and specific differences in the skulls and vertebrae of the crotalids. This has permitted the allocation to particular species of some of the fossil remains hitherto undetermined. Through his activities, as well as those of Auffenberg (1963), Holman (1958, 1959a, 1959b, 1964), and Gehlbach (1965, p. 56), the list of localities, mostly caves, fissures, mines, quarries, tar pits, etc., where identifiable Pliocene, Pleistocene, and/or Recent fossils have been discovered, now embraces the following species and localities:

*Crotalus adamanteus* (existent species)

## Florida

- Haile I, Haile VII, Arrendondo, and Wall I, Alachua County. Pleistocene and/or Recent
- Melbourne, Brevard County. Pleistocene and/or Recent
- Allen Cave, Lecanto, and Saber-tooth Cave, Citrus County. Pleistocene
- Itchtuckance Springs, Columbia County. Pleistocene and/or Recent
- Bon Terra Farm, Flagler County. Pleistocene and/or Recent
- Limerock Mine, Williston, Levy County. Pleistocene
- Reddick, Eichelberger Cave, Florida Lime Pit 2, Mefford Cave, and Orange Lake, Marion County. Pleistocene
- Seminole Field, Pinellas County. Pleistocene
- Vero Beach, Saint Lucie County. Pleistocene and/or Recent

*Crotalus adamanteus pleistofloridensis* (now extinct)

## Florida

- Seminole, Pinellas County. Late Pleistocene
- Allen Cave, Lecanto, Citrus County. Pleistocene
- 2 miles west of Melbourne, Brevard County. Late Pleistocene
- Vero Beach, Saint Lucie County. Late Pleistocene

*Crotalus atrox*

## Nevada

- Gypsum Cave, Clark County. Late Pleistocene

## New Mexico

- Shelter, Conkling, and Fosberg Caves, Pyramid Peak, Organ Mountains, Dona Ana County. Pleistocene or Recent

## Texas

- Bulverde, Bexar County. Middle Pleistocene
- Friesenhahn Cave, Bexar County. Pleistocene
- Clear Creek and Ben Franklin, Denton County. Pleistocene

*Crotalus giganteus* (now extinct)

## Florida

- Allen Cave, Lecanto, and Sabre-tooth Cave, Citrus County. Pleistocene
- Haile VII and Hornsby Springs, Alachua County. Pleistocene and/or Recent
- Eichelberger Cave, Marion County. Pleistocene and/or Recent
- Rock Springs, Orange County. Pleistocene and/or Recent

*Crotalus horridus*

## Arkansas

- Conard Fissure, near Willcockson, Newton County. Pleistocene

## Georgia

- Ladd's Lime Kiln, near Cartersville, Bartow County. Pleistocene

## Maryland

- Cumberland Cave, near Cumberland, Allegany County. Pleistocene
- Bushey Cavern, near Cavetown, Washington County. Pleistocene

## Massachusetts

- Near Greenfield, Franklin County. Late Pleistocene to Recent

Pennsylvania

- Carlisle Cave, near Carlisle (?), Cumberland County. Pleistocene to Recent
- Port Kennedy Cave, Montgomery County. Pleistocene
- Cave deposit, New Bedford County. Pleistocene

Tennessee

- Big Pigeon River, near Newport, Cocke County. Pleistocene

Virginia

- Natural Chimneys, Augusta County. Pleistocene
- Crotalus lepidus* (tentative identification based on meager material)

Arizona

- Curtis Ranch, San Pedro Valley, Cochise County, Upper Pliocene
- Crotalus mitchellii*

Nevada

- Gypsum Cave, Clark County. Late Pleistocene to Recent
- Crotalus potterensis* (now extinct)

California

- Potter Creek Cave, Shasta County. Late Pleistocene
- Crotalus scutulatus*

Mexico

- Zumpango, México (state). Pleistocene
- Crotalus viridis*

California

- Rancho La Brea Asphalt Pits, Los Angeles County. Late Pleistocene
- McKittrick Asphalt Pits, Kern County. Late Pleistocene
- Hawver Cave, El Dorado County. Late Pleistocene
- Potter Creek Cave, Shasta County. Late Pleistocene to Recent
- Mescal Cave, Mescal Range, San Bernardino County. Late Pleistocene

Iowa

- Andrews Stone Quarry, near Sioux City, Woodbury County. Pleistocene

Nebraska

- Driftwood Creek, Hitchcock County. (?) Lower Pliocene

Nevada

- Gypsum Cave, Clark County. Late Pleistocene to Recent
- Sistrurus miliarius*

Florida

- Limerock Mine, Williston, Levy County. Pleistocene
- Haile I and Haile VII, Alachua County. Pleistocene and/or Recent
- Reddick, Marion County. Pleistocene

Nearly all of these deposits occur in areas inhabited by the same species today.

Florida is especially prolific in fossil remains because of the geological conformation of some of the sites and the large size of *C. adamanteus*, which is especially likely to have left persistent records.

Other localities where undetermined (as to species) *Crotalus* fossil remains have been reported are: New River, near Ivanhoe, Wythe County, Virginia (Hay, 1923, p. 353; 1929, p. 271; Gilmore, 1938, p. 71); Mojave Desert, California (J. C. Merriam in Bryant, 1929, p. 48); Perry Township Caves, Franklin County, Ohio (Adler, 1961, p. 3); and Groesbeck Creek, Hardeman County, Texas (Holman, 1964, p. 82).

# NONFOSSIL REMAINS

Samuel Smith (1765, p. 504) reported the discovery of some "20 bushels" of snake bones in a cave near Princeton, New Jersey. They were further described as rattlesnake bones by J. Green (1821, p. 85), who stated they had been discovered in 1748.

But these, of course, are to be considered recent, rather than fossil, remains; they were probably of no great age and, indeed, may not have been rattlesnake bones at all.

### ZOÖGEOGRAPHY AND PHYLOGENY

As one becomes acquainted with the rattlesnakes, and especially with the differences in form and pattern that characterize the several kinds, there follows a natural curiosity as to the derivations and chronology of these differences. What would be the appearance of the figurative tree of historical development, if we could reconstruct its every branch? What existing forms most nearly resemble the aboriginal ancestral species that was the sapling, and what species that still persist first diverged to form the lowest branches?

Of one thing we may be sure: the major stems as we view them today—the genera *Sistrurus* and *Crotalus*—branched from a single trunk. Were this not so, it would be necessary to assume that the rattle was developed separately in each genus, and it is inconceivable that so intricate a device could have been evolved twice. And the same reasoning makes it evident that the ancestral form was plated on the crown like *Sistrurus*, rather than multiple-scaled like *Crotalus*. The nine-plate pattern of head plates must have been very primitive among snakes since it is characteristic of most genera in the widespread ophidian families Colubridae and Elapidae, which comprise the majority of the snakes in every continent. The same splitting of the head plates that characterizes the *Sistrurus-Crotalus* transition, is evident in the nonrattle branches of the family Crotalidae, that is, in *Agkistrodon* as precursors of *Bothrops* and *Trimeresurus*. Similarly, in the family Viperidae, there remain the nine-plate primitives *Causus* and *Azemiops*, in contradistinction to such genera as *Vipera*, *Echis*, and *Bitis*, all of which have many irregular scales on the crown. It is not difficult to visualize how these nine-plate patterns of the ancestral forms may have proliferated into the bewildering variations of scale arrangements found in *Crotalus*, *Bothrops*, and *Bitis*; it is impossible to conceive of the reverse process, in which the complicated could produce the simplified in *Sistrurus*, *Agkistrodon*, and *Causus*, so that these diverse ancestries not only could have evolved congruent, nine-plate crowns, but matched those of the colubrids and elapids as well.

#### ASIATIC PROGENITORS

Before outlining some of the morphological characteristics that indicate the relationships between the kinds of rattlesnakes that exist today, it is advisable to discuss the probable genesis of the group as a whole and its relationship with other families of snakes.

The rattlesnakes belong to a group known as the solenoglyphs, which is characterized by the possession of fangs attached to rotatable maxillary bones. When not in use, the fangs lie against the upper jaw along the roof of the mouth; when they are to be used for biting or striking, each maxillary rotates so that the attached fang swings downward and forward until its base is perpendicular to the upper jaw. This mechanism permits the snake to have much longer and more deeply penetrating fangs than would otherwise be possible, an advantageous feature both in securing prey and in defense.

At one time it was thought that the solenoglyphs were descended from primitive opisthoglyphs (snakes with non-movable, grooved fangs in the back of the mouth) as was suggested by Boulenger (1893-6, vol. 1, p. 2; 1896, p. 616). Now it is generally believed that the viper ancestors were proteroglyphs (snakes like the cobras, with fixed or non-erectile fangs at the front of the upper jaw) which, in turn, were derived from still more primitive aglyphs or colubrids, that is, harmless snakes without poison glands or fangs. This line of descent, i.e., aglyph-proteroglyph-solenoglyph, has been accepted by several recent workers: Bogert, 1943, pp. 314-316; Johnson, 1955, p. 386; 1956, p. 65; Dowling, 1959, p. 50; Marx and Rabb, 1965, p. 193. This consensus has been based on studies of osteology, musculature, venoms, and other features. A few herpetologists, including Haas (1952, p. 591) and Savage (1957, p. 165), still question this line of descent.

Coming now to more restricted snake categories within the solenoglyphs, most investigators agree that the Viperidae (the true vipers) were ancestral to the Crotalidae (the pit vipers). Indeed, some workers show this conclusion by separating them only at the subfamily level, considering the subfamilies Viperinae and Crotalinae as divisions of the more inclusive family Viperidae. The differences between the two seem to be limited to the heat-sensitive loreal pit, and the hollow in the maxillary bone for its accommodation, present in the crotalids but absent in the viperids. The indications of this relationship have been discussed by Bogert (1943, p. 315), Johnson (1955, p. 386; 1956, p. 60), Dowling (1959, p. 50), Brattstrom (1964a, pp. 187, 222, 249, 255), and Tu, James, and Chua (1965, p. 5).

Whatever the ancestral line that gave rise to the Viperidae, they no doubt originated in Asia, whence they spread into Europe, and also into Africa. In the latter continent they diversified into many species, particularly of the genus *Bitis*, a group, several of which are large, brightly patterned, and dangerous snakes. The true vipers, only called "true" to distinguish them from the "pit" vipers, never reached the New World, at least none has been found in that hemisphere either alive or as fossils.

#### AMERICAN INVASION

The offshoot of the true vipers, the pit vipers, not only evolved and left descendants in Asia where they are represented today by the widespread genera *Agkistrodon* and *Trimeresurus*, but also found their way into the Americas. This eastward invasion is not to be viewed as an island-hopping expedition via the Aleutians, but rather as a migration by way of a broad land corridor across the Bering Sea, a bridge that at times attained a width of at least 1300 miles, so that the travelers, including mammals, birds, and, eventually, man, made the intercontinental trip without encountering any ocean hazard. This invasion isthmus between Asia and the Americas was not a continuous one in point of time. During several geologic eras it was both established and reinterrupted. In a way, the words invasion and migration may give an incorrect impression as to the nature of the crotalid use of the Bering bridge from Asia to America, since, from these words, one might be led to infer a directional or purposeful movement. Actually at times the land comprising the bridge had such favorable qualities of climate, protective verdure, and food supply that the pit vipers merely spread into the bridge and over it until they reached the more extensive land mass of the Americas, into which they dispersed eastward and

southward. Tihen (1964, p. 273) refers to this favorable situation as an unoccupied "venomous snake adaptive zone" without competitors, which would expedite both invasion and diversification.

The snakes, of course, were not the only travelers coming out of Asia into the Americas. Not only were there other reptiles, but, more conspicuously, an amazing diversity of mammals, many large and of strange conformations, strange because they have since become extinct without living descendants. But their fossil record is clear and extensive.

The ancestral crotalids probably developed in Asia during the Cretaceous and evidently crossed into North America during the Eocene. One of the invaders must have been a snake somewhat resembling the genus *Agkistrodon* of today; at least it was a pit viper and had a nine-plate crown, as shown by its present descendants in both Asia and America. But because we have no rattlesnake fossils antedating the Pliocene, and as the rattlesnakes reach their greatest diversity of form in Mexico, there is a gap, both territorial and chronological, in our knowledge of the transition between the arrival of the primitive *Agkistrodon* in America and the proliferation of its descendants into the many rattlesnake species that we know today.

#### HISTORICAL CRITERIA

Since the fossil rattlesnake record is so meager, the historical study of rattlesnake evolution and dispersion is dependent on knowledge of conditions in the past assembled from records of other animals, and knowledge of the present based on the rattlesnakes themselves. Factors of the past include such criteria or effects as known topographic and climatic changes as determined from the paleontology of other groups of organisms, both animal and vegetable. These serve as indicators of the major forces affecting the evolution and dispersion of the rattlesnakes, especially climate and its components—altitude, temperature, and vegetation—and their probable effects on subsequent avenues of immigration and emigration. All of these factors and their presumed impacts on rattlesnake development are based largely on studies of the biogeography of other organisms which left adequate fossil records, for we may correlate their evolution and dispersal as indicators of what probably happened to the rattlesnakes coexisting with them. By the Pliocene the ancestral *Agkistrodon* had already evolved rattlesnake species not greatly different from existent forms.

The historical implications more directly derived from the rattlesnakes themselves are based on studies of two classes of criteria: first the geography and ecology of the existent species; and secondly on the indications of the relationships between these species as shown by their characteristics—their likenesses and dissimilarities.

So we see that studies of rattlesnake zoogeography are based on extra- and intra-rattlesnake history. Of the extra- (outside rattlesnake) factors I have made no independent study, but have been guided by the researches of others in these fields and their probable application to rattlesnake history. The intra-factors and effects have been derived largely from my own studies of existent rattlesnakes, and the indications of relationships derived from the physical characteristics and ecology of the living species. However, for osteological criteria I have leaned heavily on Brattstrom (1964a); and for geological interpretations on several of the recent authors whose works are listed at the conclusion of this section.

Today rattlesnakes occur from southern Canada to central Argentina and inhabit highly diversified ecological surroundings. They are most prevalent, as may be judged from the numbers of different subspecies (and probably of individuals as well) in semiarid areas and in subtropical zones. In the United States the greatest number of forms occurs in Arizona, with about 17 species and subspecies, followed by New Mexico with 12, and California with 10. And in these states, all of which have highly diverse climates and vegetation, the rattlesnakes tend to be concentrated in the drier sections. Yet the diversity of forms found in these states is not only high because they contain arid areas, but also because they are mountainous, for some of the subspecies are clearly relict populations now restricted to mountains, where they remain as remnants of formerly more widespread populations that inhabited areas once having climates and surroundings like those of their mountain habitats of today.

One safe assumption as to the features and line of descent that characterized the earliest rattlesnakes relates to the rattle itself. As is discussed subsequently in a consideration of the genesis of the rattle, we visualize, first, a modification in the conical scale terminating the tail of some early crotalid, with a likeness, possibly, to *Lachesis* of today, whereby successive sheddings were retained. Regardless of the mechanical details of how the earlier cones slipped backward in relation to the later ones, yet remained attached, it is evident that the first rattles were formed as small cones on a sharp-tailed snake. Hence small rattles and a relatively long tail are to be considered primitive. With the long tail, the primitive rattler also had more subcaudal scales than most of its descendants of today. Thus there are strong indications that the ancestral rattler had some of the characters of the existing *Sistrurus miliarius*, although it need not have been, and probably was not, so small a snake. For the theory of the evolution of the rattle that involves the protection of the snake from being trampled by primitive hoofed animals requires a more dangerous snake with longer fangs than *miliarius*.

One problem, in a phyletic survey of this kind, especially where the fossil evidence is meager, is to weigh the relative stability of characters, for those that are stable and persistent are obviously the most important in indicating derivations. Different characters are often conflicting in their indications of relationships; the subspecies A may appear to be more closely related to B than to C based on one character, but it may seem nearer to C than B based on another. We judge the comparative values of these characters from studies of intraspecific variations in existing species, especially those in which, because of extensive territorial ranges, phenotypic divergences have developed. By such means, we learn that osteological characters are relatively stable, followed, in the order of constancy, by anatomical characters (e.g., lungs and hemipenes), head and tail proportionalities, and rattle shape and dimensions. Then come the useful characters of squamation—the most attractive to the taxonomist because they are so easily evaluated, but with evidences of a considerable mutability. They are correlated with body size, in itself a phenotypic character. This correlation is not only evident in the numbers of such scales as the labials and ventrals, but may even be the cause of certain peculiarities of scale arrangement, as, for example, the loreal-supralabial contact in *C. intermedius*. Finally, we have the most plastic characters of all—those of color and pattern.

Conclusions may best be drawn respecting relationships if both similarities and

dissimilarities are noted; both should be available. Such similarities as are uniformly characteristic of all the species of a group, afford no criteria to aid in the sorting process, but similarities in subgroups are strongly indicative of origins. And the dissimilarities—the divergences—are equally important, particularly the divergences from a generic mode. But always we must consider the possibilities of reversions, of degeneration, and likewise of fortuitous parallelisms. An example of the latter is the divided first infralabial scales of *C. d. tzbacan* and *C. r. ruber*. Certainly this character does not indicate a closer relationship between these two than that between any members of the *durissus* and *atrox* groups.

Unfortunately, pairs or trios of species characterized by parallel divergences from the rattlesnake mode are less prevalent than individual species idiosyncrasies. The former are highly pertinent indicators of relationships; the latter are largely restricted to use as tools for identification. Of the latter there are examples to be found in almost every category of morphology: in cranial osteology, the shape of the ectopterygoid in *tortugensis*; in hemipenes, the smooth shaft of *stejnegeri*; in venom, the extreme neurotoxic effects of *terrificus* poison; in body proportions, the long head of *polystictus* and the long tail of *stejnegeri*; in pattern, the neck stripes of *durissus*; and, in squamation (where individualized species differences are most plentiful), the pointed supraoculars of *cerastes*, the ridged canthals in *willardi*, and many others. Fortunately, useful group divergences are also available to an important degree: in cranial osteology the absence of palatine teeth in *stejnegeri* and *polystictus*; the presence of rudimentary left lungs in *durissus*, *basiliscus*, *molossus*, and *horridus*; the attenuated hemipenes of *adamanteus*, *atrox*, *ruber*, and *tortugensis*; the similar rattle-growth equations of *durissus*, *basiliscus*, *enyo*, and *cerastes*; the head proportions of *tigris* and *m. mitchellii*; and the nine-plate crowns of *catenatus*, *miliarius*, and *ravus*. These are some of the many relationship indicators upon which a family tree may be predicated.

Little is to be gained, as far as chronoclines are concerned, from the fossil material thus far available. The three extinct forms that Brattstrom has described indicate a decrease in size of some species since the Pleistocene—*C. potterensis* was somewhat larger than is *C. v. oreganus* today; *C. adamanteus pleistofloridensis* was larger than is its Recent congener; and *C. giganteus* was far larger than any existing rattlesnake. But we may seriously doubt that large size is a primitive character among rattlesnakes. Island forms today are witnesses to the phenotypic character of size. Had the first rattlers been very large, it is doubtful that they would have adhered to the nine-plate crown; or that any of their smaller descendants would have reverted to it.

#### NOMENCLATURE AND GROUPING

In Chapter 2 of this work I developed a series of checklists and keys to facilitate the identification of the species and subspecies of rattlesnakes. This involved the principles of taxonomy and nomenclature—principles that follow certain rules whereby the technical names applied to the several kinds of creatures that comprise any animal group may have stability and consistency in application. Naming things is a matter of definite practical value; it produces a basis whereby knowledge of the animals and their activities is so segregated and unified that different workers may

apply their observations to the same creature and hence broaden our understanding of that creature. Matters of a real practical nature may be involved; for example, the several kinds of rattlesnakes differ in the toxicity of their venoms, and a recognition of the kind of rattler involved in a snake-bite accident may be of major importance in determining the best method of treatment to be afforded the victim.

One of the early expedients in a study of phylogeny and zoögeography is the fact that we are not restricted solely to a consideration of branches in the family tree that are distinguished by named groups, that is, to genera, species, or subspecies. On the contrary, the very nature of our inquiry—the picture of the family tree and its several branches—requires the consideration of groups, particularly aggregations of species, that are not segregated by any name under the rules of nomenclature. These groups, and particularly the similarity of characters that justify their recognition, are found especially fruitful in the development of the kind of family tree that we are seeking.

#### DIFFERENTIAL CHARACTERS

Species differences are rarely so sharply defined or limited in application that there is little or no overlapping. It is usual that some feature of a characteristic that distinguishes a species will be present in a few specimens of closely related species; the degree of this overlapping will often verify relationships. Such relationships are of value in tracing derivations, particularly in problems of zoögeography.

Certain trends, apparently of phenotypic origin, are evident among the rattlers, particularly in size and pattern. The largest species are lowland forms. Composite color values depend on plant cover and background. Virtually all montane forms are small and dark. At similar altitudes, the more prevalent the rainfall and the denser the shrubbery, the darker are the indigenous rattlers. Dammann (1961, p. 48) has shown that procrypsis is probably more important than relative heat absorption in determining body color, as I once judged to be the case by noting examples in which the two desirable results would have had divergent effects (1939a, p. 65) and procrypsis became dominant.

In working out these relationships we have an almost embarrassing variety of characteristics to evaluate; not only must we draw conclusions as to their relative importance in the study, but sometimes separate characters may give conflicting results and we must select the ones that seem paramount.

In this phyletic study, the following characters have been enlisted: cranial osteology (including teeth), vertebral osteology, body size, head and tail proportions, the rattle (its form and unit growth), hemipenes, lungs, venom, squamation, color and pattern, ecological preferences, and geographic range. For the osteological characteristics, I have been dependent on the recent important work of B. H. Brattstrom (1964a). The other characters are discussed in some detail in later chapters of this book.

The modern devices for comparing and establishing likenesses and relationships of organic compounds by the methods of electrophoresis and chromatography will, in the future, solve many phyletic problems of snakes, including rattlesnakes. Already results are beginning to appear, as will be noted in the following references: (1) based on *blood*, Cohen, 1951, 1954, 1955; Dessauer and Fox, 1956, 1958, 1964; Dessauer, Fox, and Ramírez, 1957; Dessauer, Fox, and Harting, 1962; Dessauer,

Fox, and Pough, 1962; and (2) based on *venom*, Boman and Kaletta, 1957; Gitter, Kochwa, de Vries, and Leffkowitz, 1957; Garcia Lopez and Sander Montilla, 1962; Jiménez-Porras, 1964; and Leviton, Myers, and Grunbaum, 1964.

Another analytic method that may prove useful in phylogeny is the determination of microscopic differences in the *stratum corneum* of the skin by the process suggested by Hoge and Santos (1958, p. 410).

#### SQUAMATION

Judging from its use in classification and especially in keys for identification, squamation, that is, the arrangements, contacts, and numbers of various scale groups, is a most useful device. The characters do suffer from some interspecific variability whereby deviants are not particularly unusual; nevertheless when species or subspecies are viewed as a group, there is often a surprising consistency in such characters.

Although, from the peculiar characters of the Mexican forms of today, their original derivations and relationships are by no means clear, yet some forms do show indicatory tendencies. This is particularly evident in the breakup of the scales in the prefrontal and frontal areas. A distinct phylogenetic pattern is evident in the transition between the nine-plate crown of *Sistrurus* and the multiple-scaled crown of *Crotalus*; and, although some of the steps in this evolution are no longer present in any living species, the nature and direction of the change may be deduced.

First the parietals were subdivided; no present species of *Crotalus* retains a pair of parietals resembling those of *Sistrurus*. The nearest remnant in a modern rattler is the crescentic pair of scales in *C. scutulatus* that border the supraoculars inwardly and posteriorly (fig. 2:110).

An undivided frontal is not characteristic of any species of *Crotalus* today; the scales of this area are divided into two or more scales between supraoculars (fig. 2:130) and they are shortened as well. Continuing forward to the prefrontal area, it is found that this alone retains in some modern species the original conformation of *Sistrurus*, namely, a pair of internasals followed by a pair of prefrontals, although relatively reduced in size.

From the phylogenetic standpoint one of the most important group characteristics is the further subdivision of these internasal-prefrontal scales. Not only is this subdivision increasingly evident in groups from south to north but it is also present within species. It is evident in the transition from *C. molossus nigrescens* to *m. molossus*, from *salvini* to *scutulatus*, from *durissus* to *culminatus*, and within *lepidus*. Characteristically, most Mexican rattlers have fewer scales on the snout than species inhabiting the United States, of which *atrox*, *horridus*, *viridis*, and their subspecies and relatives may be considered typical.

The overlapping of specific anomalies is often useful in suggesting relationships. A few examples of this type of relationship-indicator are the following:

A vertical division in the upper preocular is an almost universal characteristic of *C. lepidus*. Not only is the split evident but the anterior half of the split scale is extended over the canthus in front of the supraocular (fig. 2:94). In *lepidus* this is an almost universal characteristic; it failed in only three per cent of three hundred specimens examined. Except in *mitchellii* (characterized by the subdivision of many usually entire head scales) this *lepidus* preocular division is absent in most

other rattlesnakes. However, it is occasionally evident in the species most nearly related to *lepidus*, namely, *triseriatus* and *pricei*. This characteristic is evident in about a quarter of the northerly specimens of *triseriatus* (subspecies *aquilus*). It is less frequent in *pricei*.

The contact of the anterior subocular with the labials is a group indicator of some value. It is evident only in the smaller mountain species of Mexico; the contact is with the fourth and fifth supralabials in *triseriatus* (including the subspecies *aquilus*), in *polystictus*, and *pusillus*; the contact is with the third and fourth supralabials in the *intermedius* subspecies and in *pricei*. The subocular-supralabial contact may be present, but is rather unusual in *tigris* and in *lepidus*, especially in the subspecies *klauberi*. The contact is noted in *Sistrurus*, as might be expected in smaller rattlesnakes. It is never present in the larger species of rattlesnake, where the space between the loreal and the supralabials is too wide to permit contact.

Although we have no fossil rattlesnake remains antedating the Pliocene, this is only because such fossils rarely persist by reason of their fragility. We may assume that during, or, more probably, before that era, the *Agkistrodon*-*Lachesis*-*Sistrurus*-*Crotalus* transformation was already past its early stages and that a diversity of rattlesnake types had already evolved and had traveled at least as far as Mexico. Their subsequent character variations and territorial dispersions indicate the probability of their existence during the Tertiary from the Eocene onward. Brattstrom (1964a, p. 256) pictures them as developing and spreading in North America during the Oligocene-Miocene. Such fossil crotalids as have been available indicate that many of the present species had diversified and reached their present ranges by the Middle or Late Pliocene. The extinct ancestors of *C. adamanteus*, for example, were already present in Florida in the Pleistocene, if not before.

It was during the Pleistocene that climatic fluctuations incident to the glacial extensions and retreats greatly influenced crotalid history, forcing southerly migrations followed by shorter northerly returns, both combined with species differentiations. We see the results today in the Mexican montane forms, small in size and dark in color, but now segregated into separate species and subspecies that still show their common derivations by the retention of joint peculiarities.

#### SPECIES RELATIONSHIPS AND ORIGINS

Having discussed certain zoögeographic generalities with regard to the spread and development of the existing species of rattlesnakes, I shall now consider the probable derivations of particular species and their group interrelationships. Also the sources of the crotalid fauna of Baja California and the forms found on the Gulf of California islands will be mentioned. This is of interest with respect to the effect of island life on rattler development.

#### ZOÖGEOGRAPHY AND PHYLOGENY OF *Sistrurus*

Although considerable variability is shown in rattlesnake head scales, particularly those in *Crotalus* that entail the area of the nine-plate crown of *Sistrurus*, certain general tendencies are obvious and important. Despite the fact that an occasional specimen of *Sistrurus*, particularly of *S. ravus*, may have one or more sutures in the frontal or the parietal scales, yet there is never a real question as to whether the aberrant specimen should be assigned to *Sistrurus* or *Crotalus*; there is no full inter-

gradation between the two. It is for this reason that I prefer not to follow Brattstrom (1964a, p. 250) in assigning *Sistrurus* to a subgeneric status under *Crotalus*. I do not question the ancestral position of *Sistrurus* with respect to *Crotalus*, yet the separation remains.

*Sistrurus*, obviously primitive, has been subject to much less elaboration than *Crotalus*, since only three species are presently extant, compared to about 27 in the case of its more varied and diversified relative. Despite the seeming plasticity in the scutellation of the *Crotalus* crown, there are certain indications in respect to the direction of this variability that are of importance from the standpoint of group relationships in both phylogeny and zoögeography. This is particularly true with respect to the directional deviation from the basic nine-scale crown of *Sistrurus*.

As to *Sistrurus* itself, *S. ravus*, the most primitive species, now retains only a small range in the mountains of southern Mexico. Of the other two species, *miliarius* was one of the rattlesnakes that returned to the United States via northeastern Mexico when appropriate climatic conditions developed during the Miocene and Pliocene, after which it developed into three subspecies along the gulf coast from Texas via Florida into the Carolinas. It is interesting to note that, in *Crotalus adamanteus* and *Sistrurus miliarius barbouri*, peninsular Florida has proved a satisfactory habitat for both the largest and one of the smallest of rattlesnake species.

*Sistrurus catenatus*, a more recently developed species than either of its congeners, probably entered the United States from central Mexico later than *miliarius*. Its subsequent route across the plains, following available marshes to an ultimate terminus in western Pennsylvania and New York, evidently traversed a corridor, as suggested by Schmidt (1938, p. 400) during suitable climatic intervals of the Pleistocene. But even before the advent of the white man suitable marshlands were disappearing; and, with increased agriculture and drainage, the areas appropriate to *S. c. catenatus* were sharply curtailed. In the west the subspecies *S. c. tergeminus* and *S. c. edwardsii* have become adapted to drier areas and are surviving, but usually in small scattered populations.

#### ZOÖGEOGRAPHY AND PHYLOGENY OF *Crotalus*

As to *Crotalus*, both the character and the degree of variability of the present species indicate that Mexico was the developmental center, and that the present species, which dominate the rattlers found in the United States, with possibly one or two exceptions, do not indicate that they represent *in situ* developments along the southbound invasion route, but rather a reinvasion of later forms from the south. Indeed one of the most important of the existent rattlesnakes (*Crotalus durissus*) indicates, in the variability of its present peripheral subspecies in Mexico, that its modern components comprise a reinvasion from still farther south; if not from South America during one of the periods when the Panamanian gap was closed, at least from Central America.

By their variety and their deviations from the rattlesnake mode, one would naturally visualize central Mexico as the center of dispersal of the rattlesnakes as they exist today, both territorially and in character. The more southerly derivatives have various characteristics in common, likenesses in osteology, squamation, venom quality, and pattern. The species concerned, at least to some degree, are *durissus*, *basiliscus*, *molossus*, and *scutulatus*. As I have already pointed out, all show by the trends

in the splitting of their prefrontal scales, a migration from south to north.

A South American invasion produced an incursion of *terrificus* and other southerly subspecies of *Crotalus durissus*. Crotalids probably were early Eocene entrants into South America. As the non-rattlesnake crotalid genus *Bothrops* differentiated in Central and South America to a greater degree than did *Crotalus*, it may have been an earlier invader of the southern continent than *Crotalus*, which therefore, in the subsequent competition, gave *Bothrops* a pioneer's advantage. At least *Bothrops* differentiated more widely and utilized a more diversified ecology in South America than did *Crotalus*, while the contrary was true in Mexico. Since the Panamanian bridge was both established and reinterrupted during several geologic eras, *Crotalus* may have crossed into the southerly continent at a later time than *Bothrops*. Schmidt (1948, p. 250) has stated that the interruption of the Panamanian route continued into the Mid-Tertiary, to be followed by its later re-establishment.

*C. durissus* is much the most widespread of the southern rattlesnakes. Even though originating in Mexico or Central America, whence it invaded South America, its most recent migration has been northward, since the species on the northern fringe of its present range are clearly derivative. The history of this species still entails many doubtful elements, and its differentiation in South America contains many uncertainties (see footnote 7, chapter 2).

*C. basiliscus* of western Mexico (including *C. b. oaxacus*) has a fairly close affinity with *C. durissus*, as shown by its tuberculated scales and vertebral ridge, although it has almost lost the characteristic paravertebral stripes of *durissus*.

The relationship of *molossus* with *basiliscus* also requires further research. It is not even known whether the ranges of the two species actually overlap in Sonora or whether there is a gap between them. As their populations approach each other, some of the characters that sharply separate the two species, based on specimens at their centers of distribution, tend to be somewhat less sharply separated. However, that is not true of their hemipenial characters, which remain consistently different throughout their ranges.

*C. scutulatus* also shows certain *durissus* affinities. Its venom, apparently the most toxic of that of any Nearctic rattlesnake, probably indicates a relationship with *durissus*. But its derivation will be to a considerable extent unknown prior to the advent of more information on the subspecies *salvini*—of which too few specimens are available—to be sure whether it is ancestral or derivative, although we suspect the former relationship.

Although *C. molossus* and *C. horridus* show some obvious affinities, particularly in having rudimentary left lungs, as well as patterns that tend toward chevrons or cross-bands and in having a black tail, the relationship is not particularly close. The head scales, especially of the crown, show *molossus* to be the more primitive species. The hemipenes of *horridus* are considerably more attenuated than those of *molossus*.

*C. horridus* probably entered the United States from northeastern Mexico and spread northward through the Appalachians and along the Mississippi Valley as the climatic changes of the Pliocene and Pleistocene permitted. *C. molossus*, on the other hand, traversed the Sierra Madre foothills of northwestern Mexico into the mountains, and, to a lesser extent, the intermountain areas of western Texas, northwestern New Mexico, and southern Arizona. It avoids areas of extreme aridity.

*C. m. nigrescens* is the most primitive element of the *molossus* species, judging from the head scales and pattern. The species *molossus* is characterized by plastic tendencies of pattern and color which have led to some startlingly beautiful color variations in the several mountain ranges of the Southwest that it inhabits.

The relationship between *Crotalus adamanteus* and *C. atrox* is not so close as has often been supposed by reason of their large size, for they are indeed the largest of rattlesnakes, and as suggested by the similarity of their common names: Eastern and Western diamondbacks. At one time *atrox* was considered a subspecies of *adamanteus*. This is a relationship without validity, for they are separated territorially and their ecological preferences are quite different: *adamanteus* lives in forested areas of moderately heavy rainfall, whereas *atrox* inhabits arid plains and deserts. They are separated by the width of Louisiana and eastern Texas.

Some of their character differences are moderately evident and important. Although both have slim, attenuated hemipenes, that of *adamanteus* has a prominent patch of mesial spines, whereas *atrox* has few or none of these. *C. adamanteus* has more scales in the frontal and prefrontal areas than *atrox*, indicating a greater divergence from the ancestral form. In the patterns there are differences in head stripes and tail rings. *C. adamanteus* lacks the conspicuous tail rings, which, in *atrox*, are in strong contrast with the rest of the body; also it is without the punctated application of color so evident in *atrox*.

*C. adamanteus* probably emigrated from eastern Mexico into the gulf states and Florida at a fairly early date. Before the Pleistocene it was already established in its present range, in the form of species and subspecies now extinct; *C. giganteus* and *C. adamanteus pleistofloridensis*. And *adamanteus*, itself, was already widespread and plentiful, a conclusion we may draw from one of the few fossil aggregations of rattlesnakes that have come down to us.

*C. atrox*, as shown by the small relict populations remaining in Oaxaca and Veracruz, moved northward later, eventually occupying all the Mexican states that border the United States; and, in our own country it has ranged from southeastern Texas and central Arkansas westward to southern Arizona and the Colorado Desert of southeastern California. It shows a tendency toward a slightly reduced size and a lighter color in its progress westward into an increasingly arid habitat, but throughout its territory it remains one of the most plentiful and dangerous of rattlesnakes.

The segregation of rattlesnakes into groups having characteristics in common, yet without the restrictive taxonomic limitations affecting species, will sometimes clarify relationships and derivations. The *atrox* group, comprising *atrox*, *tortugensis*, *ruber*, *lucasensis*, and *exsul*, is an example of such an aggregation. Their similarities in morphology and pattern indicate a common derivation, yet none are to be considered subspecies of *atrox*, since they no longer intergrade with it.

Another group of species includes the dwellers of the arid areas of the southwestern United States and northwestern Mexico, in addition to *C. atrox*. These are *mittellii*, *tigris*, and *cerastes*. They clearly prefer arid surroundings, and whatever their original centers of origin and development, the climatic changes which produced the deserts of the southwest have furnished them with surroundings advantageous to them, into which they have spread and diversified. They are probably more closely related to *viridis* than to *atrox*, as determined by Brattstrom (1964a) from osteological characters.

## MONTANE RATTLESNAKES OF MEXICO

One of the most interesting features of the crotalid fauna of Mexico is the number of species of small, and usually dark-colored, rattlesnakes now restricted to mountain areas. Although each of these has generally differentiated into a number of subspecies, these subspecies are now virtually isolated from each other by inhospitable territory, so that they probably no longer intergrade. Lack of collecting in some areas, or at least an absence of specimens from critical regions, leaves a doubt as to the existence of present-day intergradation. Nevertheless the relationships are fairly clear, because of characters which are distinctive of some species and only rarely occur in others. The small species known from the mountains of central Mexico falling in this category are: *C. stejnegeri*, *C. lannomi*, *C. polystictus*, *C. triseriatus* (2 subspecies), *C. intermedius* (3 subspecies), *C. transversus*, *C. pusillus*, *C. lepidus* (3 subspecies), *C. pricei* (2 subspecies), and, more distantly, *C. willardi* (4 subspecies). This array comprises nearly a quarter of all the known forms of rattlesnakes. They must have evolved and spread in central Mexico under ecological conditions, particularly of climate and topography, that permitted a widespread occupancy of a territory. The restriction to montane islands, the present situation, must have been a later development, coincident with climatic changes and mountain building.

Some of these montane forms in central Mexico have characters indicating that they are the most primitive of the existent species. Included in this category are, especially, *stejnegeri*, *lannomi*, *polystictus*, and *pusillus*. *C. willardi* is also peculiar, but its individualities are less primitive.

*C. stejnegeri* is a peculiar rattlesnake with a limited range in southeastern Sinaloa and western Durango. Its tail is proportionately longer than that of any other rattlesnake (except possibly *lannomi*) and the adult rattle is smaller, as would be consistent with a slim, tapering tail. In its hemipenial character *stejnegeri* is unique among the rattlesnakes, with a slim, smooth shaft, more fully described on p.000. Because of its limited range in a relatively inaccessible area, only five specimens (four males and one female) are at present available in study collections.

The lance-headed rattler, *polystictus*, another individualistic species, is especially noted for its slim head, and for scale and pattern anomalies, such as the thin paired intercanthals and slender dorsal scales on the back. It has a dorsal pattern of longitudinal ellipses. Its present range is not known with finality; some early experiences by collectors indicated that it may once have been partial to an aquatic existence.

*C. pusillus* is a species having head scales of a more primitive composition than those of the more widespread Mexican mountain forms. In this character it is more primitive than *stejnegeri*.

*C. willardi* is a mountain form, which, although deemed ancient by reason of the extended territory that it occupies, and the number of subspecies that have been evolved, nevertheless has a head scalation quite at variance with the other, more primitive, montane forms. It is characterized by canthal and internasal ridges that are quite unrattler-like in form. Also, the scales of the frontal and prefrontal areas are reduced in size (and correspondingly increased in number) to an extent quite unlike those of other mountain rattlesnakes.

## ORIGIN OF SPECIES CENTERING IN THE UNITED STATES

One of the major questions concerning rattlesnake zoögeography has to do with the origin of the species whose present centers of population lie in the United States. Were they originally Mexican, proceeding northward as the retreat of the glaciers permitted; did they develop from essentially Mexican species; or do they represent species whose dominant ranges have always been in the United States?

Of all the species of rattlesnakes now inhabiting the United States, the one that presents the most valid possibility of having developed during the southerly migration of *Agkistrodon* and the rattlesnake progenitors, from the Bering bridge to the area of evolution and proliferation in Mexico, is the species *Crotalus viridis*. For this species and its derivatives now inhabit the territory which the southbound invaders must have traversed. However, there is one objection to any theory of *in situ* development, which is that *viridis* is not sufficiently primitive. Or, if this program of development was in accord with what happened, the ancestors of the present *viridis* must have gone through the same stages of development and diversification that the other species did in Mexico before their northward re-entry from the subtropics.

The head scales of *viridis* show a wider separation from the primitive *Sistrurus* and the early forms of *Crotalus* than do the species whose headquarters remain in Mexico. All subspecies of *viridis* exhibit to a major degree a characteristic peculiar to them, namely, having more than two internasals, the normal number in all other rattlesnakes. Further, the scales elsewhere on the crown are relatively numerous, which is characteristic of rattlesnakes of comparatively recent development. The answer to this uncertainty seems to be that the ancestral *viridis* did develop and change to its modern form in a Nearctic area, following somewhat the same type of change as that sustained by the other species that reached the subtropics and evolved there. And, having attained the characters resembling those of its southern neighbors, probably in the Miocene or Pliocene, it subsequently extended its range into the large area from the Missouri River basin to the Pacific Coast that it now occupies.

The area of greatest uniformity of *viridis* is in the midwest. Some of the connections between subspecies are rather tenuous and uncertain, such as those between *viridis viridis* and *v. oreganus*, and between *nuntius* and *cerberus*, for example. It is not impossible that some of the newer methods of blood and venom studies may eventually indicate that the forms which we now consider *viridis* subspecies may really belong to two or more different species, and this despite the confirmatory evidence of the internasals. But however this may be, the development of the *viridis* complex *in situ* remains a strong probability.

Besides its own subspecies, *viridis*, when it met the extreme arid conditions of the Mojave and Colorado deserts, also probably became, as Brattstrom (1964a) believes, the progenitor of such xerophilic forms as *mitchellii*, *tigris*, *cerastes*, and even *enyo*.

## ISLAND RATTLESNAKES

The islands of the Gulf of California present an interesting example of rattlesnake dispersion, or at least water-borne dispersion, as these islands lie in a long gulf between two stretches of Mexico, one of which comprises the long slender peninsula

of Baja California, and the other the shores of the states of Sonora and Sinaloa. Since these two Mexican areas on the two sides of the Gulf contain a number of species of rattlesnakes not common to both sides, their distributions on the islands between are of considerable zoögeographical interest.

The islands are scattered through the Gulf of California at varying distances from both shores, although the majority are nearest to the peninsula, or western shore. They are also of diverse sizes, so that one may judge the effect of island area on speciation and the rapidity of character change through isolation.

On the Pacific Coast of the peninsula there are fewer islands than in the Gulf. These extend up to the coast of California; their rattlesnake inhabitants also show some interesting modifications from their mainland forebears. Altogether these island residents, either of the Gulf of California or of the Pacific shore, comprise a more varied complex and thus a more interesting study than the rattlers inhabiting the islands off Florida and Texas. The latter show less variability since there are fewer parent species on the mainland, whence they emanated.

Rattlesnakes are by no means the only reptiles found on the Mexican islands, most of which are inhabited by numerous species of lizards and by other snakes (Soulé and Sloan, 1966; Dixon, 1966). And these islands have the further interest of a geologically violent history, particularly during the Pleistocene, when several distinct glacial epochs affected both the climate and the sea level. The latter varied by as much as 350 feet, and many of the present islands were connected to the mainland either to the east or west during comparatively recent times, geologically speaking.

Whether the rattlesnakes now inhabiting the islands first arrived by swimming, were carried on rafts of debris, or invaded the islands by former land connections cannot now be determined. The affinities of the islanders are usually with the present dwellers of the mainland areas nearest the islands, but this would generally be true regardless of their means of access. The swimming ability of rattlesnakes (see pp. 496–504), particularly in water at temperatures that prevail in the Gulf of California, is such that either swimming or rafting could well account for the presence of the snakes on the islands. But the prevalence of other, smaller reptiles, whether lizards or snakes, many more delicate than rattlesnakes, would seem to favor either rafts or direct land connections as the avenues of colonization. Further, the distributions are too extensive and too uniform to favor the chances of such sporadic and hazardous means as rafts and would suggest the probability of direct invasions by land connections.

There is considerable variability in the degree of differentiation of the rattlesnakes inhabiting the islands from their congeners on the nearest mainland. At the present time only two forms living on Gulf islands have been given the status of full species: these are *Crotalus catalinensis* and *C. tortugensis*. The rest of the islanders are considered either identical with mainland forms, or, at most, subspecies.

The islands of the Gulf are mostly of a rocky, desert character, but are usually inhabited by small mammals and lizards, affording an adequate food supply for any rattlesnakes that might gain access to them. Of the islands having areas exceeding about a quarter square mile, of which there are some 28, 17 are tenanted by at least one species of rattlesnake. Five of these have two species, and the islands of Tiburón and San José three each.

Judging by relationships, the most adept colonizers are *C. atrox*, found on four islands (not including its descendant on Tortuga), *C. enyo* on five islands, *C. mitchellii* on eight, and *C. ruber* (including the subspecies *lucasensis*) on five.

If we assume that, when an island rattlesnake is similar to, or most closely related to, a species occurring on the nearest mainland, a direct land connection was probably the means whereby the island was originally colonized, 24 out of 26 of the island tenancies fall within this category. In only one instance is the island form most closely related to a species occurring on the more distant of the two Gulf shores, thus indicating swimming or rafting as the probable means of access. The case is *C. atrox* on Santa Cruz Island, which is an outstanding exception to the rule of relationship concordant with propinquity.

Four other cases require some discussion. San Esteban Island, which harbors a subspecies of *C. molossus*, is actually nearer Baja California (where *molossus* does not occur) than to Sonora. However, it is adjacent to Tiburón, a large island close to Sonora and clearly extending certain faunal elements of that state, including *molossus*. Another island where *atrox* is found is San Pedro Mártir, slightly nearer Baja California than Sonora, but this island is also closer to Tiburón than to Baja California.

Two other forms require special consideration. These are *C. tortugensis* on Tortuga Island, about halfway between the two coasts, and *C. catalinensis*. The former, an obvious derivative of *C. atrox*, has differentiated sufficiently to be considered a separate species.

*C. catalinensis* is the most peculiar of all. It occurs only on a small island close to the Baja California shore toward the southerly end of the Gulf of California. Although having some characteristics that might relate it to *C. atrox*, its closest relative seems to be *C. scutulatus*, a snake not occurring in Baja California and not close to the shore of either Sonora or Sinaloa, except at a point near Bahía San Jorge, toward the head of the Gulf, and about 450 miles from Santa Catalina Island.

Of the instances wherein the island derivation correlates well with propinquity, there is *C. cerastes* on one island, *C. enyo* on 5, *C. mitchellii* on 8, and *C. ruber* on 5.

As to the genesis of the rattlesnakes that inhabit the two sides of the Gulf of California—that is, Sonora and Sinaloa to the east, and the peninsula of Baja California to the west—and which have become island invaders, *molossus* emanated from the mountains of Mexico to the southeast, and the desert forms *atrox* and *cerastes* from the desert areas to the east or north.

The Baja California forms originally came down from the north. Those with the most doubtful histories are *C. ruber* and *C. enyo*. *C. ruber* is undoubtedly derived from *C. atrox*; the relationship is shown by many common characteristics such as cranial osteology, hemipenes, and pattern and color. Although the Cape San Lucan form of *ruber*, that is, the subspecies *lucasensis*, appears in some characteristics nearer *atrox*, than is *ruber ruber*, it is to be doubted that *ruber* worked its way up the peninsula into California from the Cape. Rather it is to be assumed that *ruber* differentiated from *atrox* in the desert mountains of southern California and, after such diversion, became separated from the main body of *atrox* by the extension of Lake Cahuilla or one of the predecessors of that body of water in the area of the Colorado Desert. Subsequently when dry land was re-established, *ruber* and *atrox* again contacted each other, but without intergradation, as is the situation today

in the desert mountains to the west of Palm Springs and Palm Desert, Riverside County, California.

As to *C. enyo*, Brattstrom considers this, by reason of certain osteological characters, a derivative of *C. viridis*, in one of its California forms. Of this, I remain somewhat doubtful. *C. enyo* appears to me to possess certain characteristics of head scales, scale protuberances, and vertebral ridge that indicate a possible relationship with *C. durissus*. If we presume a trans-Gulf invasion of the cape region of Baja California by the ancestral *C. enyo* this might account for this peculiar species. I admit that the intermittent flooding of southern Baja California during the late Miocene or Pleistocene tends to negate this theory of origin, and that *C. enyo* probably did come down from the north as presumed by Brattstrom (1964a, p. 245).

In size, the island rattlesnakes, whether of the Gulf of California or of the islands of the Pacific coast of the Californias, are somewhat dwarfed but not conspicuously so. That is, although they seem never to reach the extreme lengths attained by their mainland congeners, still the size differences are moderate, as if their smaller populations failed to produce the extremes in size found among the larger populations of the mainland.

To this general statement there are three notable exceptions: two dwarfs and one giant. The former are *C. mitchellii muertensis* of El Muerto Island in the Gulf of California and *C. viridis caliginis* of South Coronado Island off the northwestern coast of Baja California in the Pacific. Both of these subspecies are markedly stunted compared with their mainland ancestral forms. In both instances sufficient specimens of the island taxa have been collected to prove that the size difference is not due to the caprice of sampling. Both of the islands on which these stunted forms occur are small, only a fraction of a square mile in area.

The other deviant from the rule of a moderate diminution in extreme size is a still more remarkable case. This is *C. mitchellii angelensis*, an inhabitant of the large (510 sq.mi.) Angel de la Guarda Island at the northern end of the Gulf. The snakes of this subspecies attain a size not reached by any other snakes of the species *C. mitchellii* anywhere in its considerable range in Baja California (where it is found throughout the peninsula) or in California, Nevada, Utah, or Arizona. Again, this peculiarity of gigantism among the island snakes is not a chance hazard of sampling but is verified by extensive collections. Nor does it occur on any of the 8 other islands on which *mitchellii* is found, one of which is on the Pacific coast of Baja California.

#### FAMILY TREE

The family tree presented in figure 3:4 represents the result of applying the methods I have outlined to the raw material of the morphological and statistical data on the rattlesnakes. As has been stated, osteological characters are deemed relatively stable and therefore of importance in the determination of major branches; however, all characters have been given due weight, so that the tree differs in the positions and directions of the branches from that which would have been evolved solely from osteological trends. For the osteological data and comparisons, I am indebted to B. H. Brattstrom, particularly his paper 1964a.

No attempt has been made in this tree to indicate geographical relationships or proximities. The lengths of the branches are only slightly indicative of the chronol-

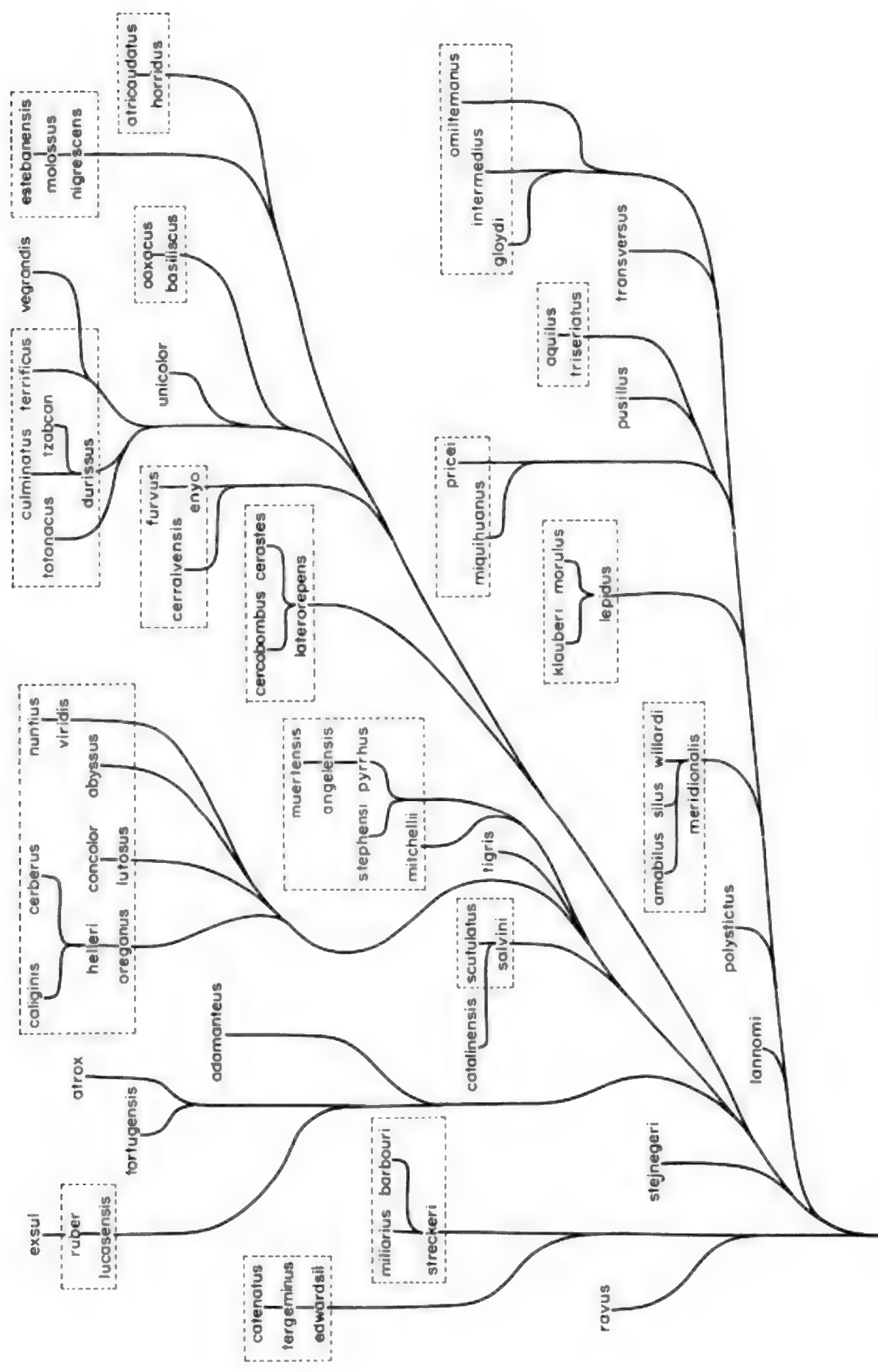


Fig. 3:4. Phylogeny of the rattlesnakes, genera *Crotalus* and *Sistrurus*.

ogy of separations and divergences, since the primary purpose of the tree is to indicate morphological relationships. Primitiveness is indicated by relative points of attachment of branches rather than by the lengths of the branches; that is, branch lengths are drafting conveniences. To the extent that one branch diverges from a main stem before another, there is an indication of chronology, but the length of the stem between branches is not based on a rigid time scale.

All of the names entered in figure 3:4 are the names of subspecies, wherever a species has been subdivided. However, the subspecific components of each species are indicated by surrounding dotted lines. Where one subspecies is apparently a direct descendant of another, this is appropriately indicated by a line through the one to the other.

It must always be remembered that the morphology of an ancestral form at the time of its divergence was probably quite different from that of its descendants of today. Only territorial isolation caused the divergence to become complete. At every branch point we must visualize a prototype having the primitive characters capable of evolving into all of the components beyond the branch point.

A subspecies that is widespread and flourishing is, of course, not necessarily to be considered the stem from which the other members of the species branched. The relative number of characters in which each subspecies differs from the specific mode is important, as well as are the clines in those characters. And one must avoid an unconscious assumption that the nominate subspecies is ancestral, since the possession of the name is often merely an accident of discovery and nomenclature.

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## 4. Morphology



### INTRODUCTION

This chapter treats of the sizes and bodily forms of rattlesnakes. There is first a discussion of the sizes and weights attained, with stress on the largest species, as a matter both of popular interest and of importance in the relative danger from snake bite. Some kinds of rattlesnakes grow to a length three or more times that of the smallest species, which means that they exceed them in weight by 50 times or more.

There follows a discussion of body proportions, particularly of head and tail lengths, in which, likewise, there are notable species differences, as well as similarities, that verify relationships.

Scales and scale arrangements are dealt with at length, for these are of importance in rattlesnake classification. Here it has been necessary to use technical terms extensively, for only in such terms can the scale arrangements and species differences be described succinctly. One might suppose it to be easy to recognize and differentiate the various kinds of rattlesnakes by appearance, especially by their colors and patterns. Those of long experience can do this with a moderate degree of success; but a number of kinds of rattlers are superficially much alike, yet from their scales we know them to be quite different creatures. Patterns and colors are found to be variable within a single subspecies, which may, for example, be gray in one part of its range and pink in another. But scale arrangements are more consistent, and it is only through knowledge of the scales and their nomenclature that the different kinds of rattlers can be correctly identified. Thus, the keys to identification, as set forth in chapter 2, are largely based on scale differences. It is not difficult to become familiar with the scale names and arrangements through the use of the glossary and sketches that have been supplied. Certain generic correlations between groups of scales, and between these groups and body size, are also of interest.

There follows a discussion of colors and patterns, with a summary of species differences and resemblances in these rather variable attributes. The chapter closes with a survey of exceptional or freak rattlesnakes, such as hybrids, two-headed snakes, and albinos.

The rattles are the only unique morphological feature of the rattlesnakes, setting them apart from all other kinds of snakes. In chapter 5, I have described the rattles fully, from the aspects of use, development, and form.

## LENGTH

Few rattlesnake characteristics are of greater interest to the average person than size. When a rattlesnake story is told, the size of the snake is always an important feature. And, from a practical standpoint, size is of significance, for several elements of the relative danger from rattlesnake bite vary with size, such as the distance a snake can reach in its strike, the length of the fangs, and the quantity of venom discharged. Rattlesnake species differ greatly in size. Some of the smallest kinds rarely attain an adult length of 2 feet, whereas others may reach 6 feet or more. Even these figures give a rather inadequate idea of the size differences, for the larger snakes have a bulk or weight of from 30 to 50 times that of the smaller.

As is the case with all animals, there is a considerable variation in the size of the adults in any population of rattlesnakes within a single subspecies. The nature and extent of this dispersion have been discussed elsewhere (p. 325). It has been pointed out that there is not only a population variability, similar to the differences in the heights of the men comprising any group, but also there are regional differences within subspecies—differences below the level of nomenclatorial recognition. For example, the prairie rattlesnakes of central South Dakota are, on the average, larger than those of eastern Colorado, although both are considered to belong to the subspecies *Crotalus viridis viridis*. Such territorial differences are the rule in wide-ranging subspecies, or in those that inhabit diverse ecological areas.

These regional differences in size impose difficulties in determining subspecific standards or bench marks. In addition, there are practical difficulties. Rattlesnakes can be measured accurately only "in the round," for skins stretch so much—up to 35 per cent—that any measurements based on skins are quite valueless. It is almost impossible to measure the lengths of live rattlesnakes accurately, especially the large specimens that would be of the greatest interest. The most accurate measurements are those made on snakes just after killing for preservation, but before they have stiffened; at this time they can be laid out along a ruler and measured exactly. Unfortunately, the difficulties of preserving large rattlesnakes, involving cumbersome containers and much preservative, are such that preserved collections seldom represent fair population samples of the larger species; and the record-breakers especially, of which it would be of decided interest to have the measurements, are never available. Mere estimates of the lengths of live rattlesnakes are quite useless; amateurs almost invariably overestimate the lengths to a marked degree; and even experienced observers can rarely guess the length of a snake within 10 per cent of actuality.

These difficulties of securing accurate data on rattlesnake lengths have been often mentioned (e.g., Metcalfe, 1907, p. 124; Strecker, 1929b, p. 10; Klauber, 1937, p. 4). Impressions concerning the lengths attained by rattlers in particular areas are likely to be greatly exaggerated. Bailey (1905, p. 50) was told, when he began certain biological investigations in Texas, that rattlers 11 to 13 feet in length were found

there, but the longest he encountered was 4 feet 2 inches. However, it is true that western diamonds slightly exceeding 7 feet have been found in Texas.

#### INTERSPECIFIC COMPARISONS OF LENGTH

In order to indicate the relative sizes of different species and subspecies of rattlesnakes, one must decide upon certain representative age or size criteria—that is, landmarks for each species—at which the comparisons may be made.

The first of the size categories that I have used is the size of the smallest specimen that I have measured, provided it was known to have been born alive, and was not obviously a freak. However, if the smallest available specimen representing one of the rarer species had more than a button in its rattle string, thus showing that there had been some growth before measurement, the figure for that subspecies has been omitted as being of little value. The available data are set forth in column 1 of table 4:1.

The second column presents the estimated average size at birth, based on all the available broods or juveniles, together with my knowledge of the general character of the species. Although a subjective figure, the average size at birth is probably rather accurate, especially in the case of the more common species, of which many broods and single-rattle young have been available.

The third column contains somewhat fragmentary information on the minimum sizes of females found to contain embryos or developing eggs. Where adequate series have been at hand, this gives a fair indication of the lower limit of adult female sizes. However, it must be remembered that the young females of most species carry their first eggs for some nine months (including three to six months of hibernation), while still at an age when rapid growth is taking place. Indeed, some species—the prairie rattlesnake (*C. v. viridis*) in the Missouri Basin, for example—live in unfavorable climates permitting such short seasons of activity that they cannot bring their young to term in a single season and so must carry a clutch of eggs for nearly two years. Thus this criterion of length is, at best, a rather indefinite datum. Studies of the subspecies of which adequate series are available indicate that the smallest females have a length of about 60 per cent of the large males and 67 per cent of the largest females. They are, when first gravid, about two to two and a half times their own lengths at birth.

In the fourth column there is presented the length of what I have chosen to call a large adult male. This is a subjective figure based on experience. As has been pointed out elsewhere (p. 324), snakes do not attain a sharply defined discontinuance of growth when they reach adulthood, at least as determined by sexual maturity; on the contrary, they continue to grow for a considerable time but at a decremental rate. Thus, we have not only the usual individual variations common to all kinds of animals, but a less sharply defined adult size in each individual. I have sought to overcome these uncertainties by fixing, based on my experience with each subspecies and the measurements that have been accumulated, the probable average lengths of the male rattlesnakes comprising the upper 2 to 4 per cent of the adult male population.

The next column gives, for each subspecies, the length of the largest specimen that I have measured. These are almost always males, for the fully adult males exceed the females in length by about 15 per cent in all species except the side-

winder (*C. cerastes*). True, a few of the records of other species—as indicated in the table by appropriate footnotes—are held by females, but it is believed that this apparent discrepancy results from the inadequate number of specimens at hand.

The last column contains the largest reliable report—when not of my own measurement—in the case of a few species so large in size that the maximum specimens obtainable in the field are rarely or never preserved. Admittedly, there is difficulty in assessing the reliability of such reports, whether published or contained in letters that I have received.

I have deemed it advisable in this table to restrict the measurements entirely to millimeters. To convert to inches, divide by 25.4 or multiply by 0.03937. As a matter of fact, multiplying by 0.04 will give an answer as close as the data warrant.

I have already mentioned intrasubspecific territorial differences in length. In general, the tabular data are presumed to indicate approximate lengths in those areas wherein the species or subspecies attains its maximum size—*atrox* in Texas, *viridis viridis* in Montana, for examples. However, in the case of *nuntius* the opposite is true; the table represents *nuntius* in the Winslow, Arizona, area, where it is smallest and most sharply differentiated from *viridis viridis*.

As might be expected, there is a quite consistent generic relationship between rattlesnake lengths at birth and the lengths attained by the large males of the same species, as set forth in table 4:1. Plotting the pairs of values in a scatter diagram, we find that all subspecies adhere quite closely to a curve—a parabola—the equation of which is found to be  $B = 37.0 + 0.263L - 0.0000521L^2$ , where  $L$  is the adult male length and  $B$  the average length at birth, both expressed in millimeters. The curve is of interest in showing that the smaller kinds of rattlers are, relatively speaking, longer at birth than the larger kinds. For example, using this generic trend curve, we find that a species having an ultimate length of 600 mm. would have a length at birth of 176 mm., so that it multiplies its length at birth by only 3.41 in attaining full growth, whereas a large species reaching 1,700 mm. would have a length at birth of 333 mm., a growth ratio of 5.11. It is to be noted that island and other stunted forms grow proportionately less up to maturity than their larger congeners; thus dwarfing is to be considered in part a postnatal development. However, dwarfs do not depart from the generic curve to any greater extent than other forms.

The most conspicuous deviators from the generic curve are the subspecies of *C. cerastes*, which are proportionately somewhat larger at birth than most rattlesnakes; and the species of *Sistrurus*, as well as *C. intermedius*, *C. pusillus*, and *C. pricei*, all of which are smaller. One may hazard the guess that the sidewinder deviation is related to the fact that this is the only rattlesnake species in which the adult females exceed the males in size.

#### MAXIMUM RECORDS

The maximum sizes reached by some of the largest rattlesnakes deserve a more complete treatment than has been given in the tabular matter already cited, for this is a feature of rattlesnake life having wide popular interest.

It must be admitted that there is difficulty in drawing a line between obviously mythical or fantastic reports and those that have at least some semblance of truth

TABLE 4:1  
DATA ON RATTLESNAKE LENGTHS  
(All measurements in millimeters)

Subspecies	Smallest measured specimen <sup>a</sup>	Average size at birth	Smallest gravid female	Large adult male <sup>b</sup>	Largest measured specimen <sup>c</sup>	Maximum report believed reliable
<i>C. adamanteus</i> .....	353	350	...	1,850	1,820	2,440
<i>C. atrox</i> .....	257	330	742	1,700	1,685	2,130
<i>C. basiliscus basiliscus</i> .....	296	330	972	1,700	2,045 ♀	.....
<i>oaxacus</i> .....	...	...	...	1,000	905	.....
<i>C. catalinensis</i> .....	...	...	...	.....	731 ♀	.....
<i>C. cerastes cerastes</i> .....	171	175	485	550	587 ♀	.....
<i>cercobombus</i> .....	221	185	440	600	628 ♀	.....
<i>laterorepens</i> .....	189	190	478	640	824 ♀	.....
<i>C. durissus durissus</i> .....	314	315	...	1,600	1,695	1,800
<i>culminatus</i> .....	331	315	...	1,600	1,680	.....
<i>terrificus</i> .....	277	305	...	1,400	1,406	1,525
<i>totanacus</i> .....	352	315	...	1,600	1,632 ♀	1,665
<i>tzabcan</i> .....	...	315	...	1,600	1,555 ♀	1,688
<i>C. enyo enyo</i> .....	207	225	608	850	898	.....
<i>cerralvensis</i> .....	...	...	...	.....	778	.....
<i>furvus</i> .....	...	...	...	.....	740	.....
<i>C. exsul</i> .....	...	240	727	900	940	.....
<i>C. horridus horridus</i> .....	279	285	887	1,250	1,195	1,880
<i>atricaudatus</i> .....	370	300	1,138	1,450	1,476	1,892
<i>C. intermedius intermedius</i> .....	178	150	317	500	570 ♀	.....
<i>gloydi</i> .....	183	150	...	530	518 ♀	.....
<i>omiltemanus</i> .....	173	160	392	550	560 ♀	.....
<i>C. lannomi</i> .....	...	...	...	.....	638 ♀	.....
<i>C. lepidus lepidus</i> .....	170	190	441	650	715	770
<i>klauberi</i> .....	166	195	390	670	828	.....
<i>morulus</i> .....	225	190	470	650	720	.....
<i>C. mitchellii mitchellii</i> .....	...	240	797	940	939	.....
<i>angelensis</i> .....	...	265	649	1,300	1,367	.....
<i>muertensis</i> .....	...	185	431	620	637	.....
<i>pyrrhus</i> .....	270	260	573	1,000	1,114	.....
<i>stephensi</i> .....	234	230	674	870	943	.....
<i>C. molossus molossus</i> .....	291	280	703	1,200	1,257	.....
<i>estebanensis</i> .....	...	...	732	980	982	.....
<i>nigrescens</i> .....	250	270	742	1,150	1,092	.....
<i>C. polystictus</i> .....	258	230	537	850	930 ♀	.....
<i>C. pricei pricei</i> .....	159	160	301	550	640	.....
<i>miquihuanus</i> .....	...	...	...	.....	532	.....
<i>C. pusillus</i> .....	200	175	...	620	674	.....
<i>C. ruber ruber</i> .....	299	300	733	1,400	1,524	1,625
<i>lucasensis</i> .....	273	290	736	1,300	1,306	.....
<i>C. scutulatus scutulatus</i> .....	220	265	630	1,100	1,231	.....
<i>salvini</i> .....	...	250	...	1,000	932	.....
<i>C. stejnegeri</i> .....	282	170	...	600	614	.....
<i>C. tigris</i> .....	307	210	616	770	885	.....
<i>C. tortugensis</i> .....	...	250	762	1,000	1,058	.....
<i>C. transversus</i> .....	183	150	...	500	459	.....
<i>C. triseriatus triseriatus</i> .....	151	175	453	620	683	.....
<i>aquilus</i> .....	172	175	340	620	678	.....
<i>C. unicolor</i> .....	230	235	...	950	920	.....
<i>C. vegrandis</i> .....	...	...	...	.....	636	684

TABLE 4:1—Continued

Subspecies	Smallest measured specimen <sup>a</sup>	Average size at birth	Smallest gravid female	Large adult male <sup>b</sup>	Largest measured specimen <sup>c</sup>	Maximum report believed reliable
<i>C. viridis viridis</i> <sup>d</sup> . . . . .	212	270	890	1,150	1,206	1,448
<i>abyssus</i> . . . . .	260	250	684	1,000	980	.....
<i>caliginis</i> . . . . .	220	190	528	650	683	.....
<i>cerberus</i> . . . . .	287	255	701	1,050	1,032	.....
<i>concolor</i> . . . . .	212	205	522	750	735	.....
<i>helleri</i> . . . . .	225	275	596	1,200	1,371	.....
<i>lutosus</i> . . . . .	242	265	557	1,150	1,210	1,346
<i>nuntius</i> <sup>e</sup> . . . . .	233	180	395	650	732	.....
<i>oreganus</i> . . . . .	221	270	503	1,150	1,320 ♀	1,626
<i>C. willardi willardi</i> . . . . .	189	165	481	560	593	.....
<i>amabilis</i> . . . . .	...	...	...	...	582	.....
<i>meridionalis</i> . . . . .	233	165	...	560	562 ♀	.....
<i>silus</i> . . . . .	184	170	452	590	647	.....
<i>S. catenatus catenatus</i> . . . . .	167	220	405	850	935	952
<i>edwardsii</i> . . . . .	...	...	...	...	530	.....
<i>tergeminus</i> . . . . .	178	215	535	800	820	.....
<i>S. miliarius miliarius</i> . . . . .	170	160	437	530	535	.....
<i>barboursi</i> . . . . .	176	170	390	630	707	788
<i>streckeri</i> . . . . .	154	165	360	630	638	.....
<i>S. rarus</i> . . . . .	174	175	505	620	699	.....

<sup>a</sup> Known to have been born alive. Probable freaks omitted.  
<sup>b</sup> Of the order of the 2 to 4 largest males to be found in a group of 100 adult males; in the case of the *cerastes* sub-species, the largest are normally females.  
<sup>c</sup> Females are marked ♀; in all other cases the largest measured individual was a male.  
<sup>d</sup> Montana only, where the subspecies probably reaches its maximum size.  
<sup>e</sup> Winslow, Arizona, area only, where the subspecies is most typical.

or accuracy. An unreliable report may recur in print so often—usually without acknowledgment of the original source—that it acquires, through mere persistence, a quite undeserved authenticity. Many of the older records represent only the repetitions by overcredulous travelers of campfire tales—the creative exercises of some hunter or cowboy spoofing a tenderfoot. These lengths usually reach such proportions—10- to 20-foot rattlers—that they deserve no serious consideration; a few of these mythical records have been mentioned elsewhere (p. 1264).

Undoubtedly many of the supposedly authentic records have resulted from the measurements of skins, a thoroughly unreliable basis, since a skin, whether preserved flat or by stuffing, readily stretches from 25 to 35 per cent. In one instance, a famous snake authority secured a notable record from a field man, who, the authority thought, was familiar with the inaccuracy involved in measuring skins. The field man was trustworthy and there was no attempt to deceive, but unfortunately he was not acquainted with the unreliability of skin measurements, with the result that, with the best intentions, another quite unauthentic record has persisted through a number of texts. A less important source of error is the measurement of a rattlesnake to the tip of its rattle, rather than to the base; however, this will lengthen the record by only 4 or 5 inches at most.

It is true that persecution may have reduced the sizes attained by rattlesnakes in some areas near human habitations. In the case of such a commercially important animal as the alligator, this has undoubtedly been true in most areas in the southeastern United States. Bartram, as long ago as 1791 (p. 263), thought the

same to be the case with the rattlesnakes of that region; and several of my correspondents have cited this as the reason why the current run of rattlesnakes in their districts do not achieve the lengths formerly reported. W. T. Neill informed me that in northern Florida there had been a consistent reduction in the average size of the adult eastern diamondbacks (*C. adamanteus*) secured by Ross Allen during the past 20 years. Formerly 5½-foot snakes were plentiful; now the average is 4 to 4½ feet. These statistics were based on about 2,000 specimens per year. As I have said, this is undoubtedly true in populous areas, but rattlesnakes, being both small and secretive creatures, do not require very large primitive spaces in order to live almost undisturbed lives. It is probable that in the case of every large species, individuals as large as any that existed in the recent past ought still to be found in the more remote parts of their ranges.

Finally, there is the normal variation in size within any population group. Just as we see exceptionally tall men in basketball teams and sideshows, so also there are rattlers much larger than their fellows. But I doubt whether a rattler exceeding its fellows by 50 per cent is much more common than an eight-foot man. This transfers to the mythical any rattlesnake approaching a length of 10 feet. Having mentioned some of the possible inaccuracies surrounding the reports of very large—but not mythical—rattlers, I shall list (but without guarantee) a few reports of record-breaking sizes among the largest species. I shall also mention how the record-breakers compare with the usual run of the same species.

*Eastern Diamondback.*—*Crotalus adamanteus* is the largest of the rattlesnakes. Specimens exceeding 7 feet (2,134 mm.) in length are well authenticated, although I cannot claim to have measured one myself, and 8- and 9-foot snakes (2,348 to 2,743 mm.) have been reported, possibly with some basis of truth.

In 1953, E. Ross Allen, of Silver Springs, Florida, wrote me:

I have been in business for nearly 28 years, during which time I have received from 1,000 to 5,000 *Crotalus adamanteus* annually, a total of about 50,000 altogether. The largest specimen I personally measured was 7 feet 3 inches in total length, exclusive of rattle, and weighed 15 pounds. For years I offered a reward of \$100 to anyone who brought in an 8-foot Florida diamondback, dead or alive. In recent years I have offered \$200, without results. This reward still stands; I doubt that it will ever be claimed. Very few 7-footers have been received. I have seen a number of 8-foot skins; but a skin this length may be taken from a 6-foot snake. I may add that for years I have subscribed to a clipping service which provided copies of newspaper articles about snakes. The killing of a diamondback often receives mention in the local newspapers; no 8-foot specimen has been reported.

Using 7 feet (2,134 mm.) as the lower limit of eastern diamonds worthy of comment, even though snakes of this length are quite rare, we have the following reports to record: Webb (1888, p. 271) mentioned a specimen that measured 7 feet 8 inches (2,337 mm.), when hung up to be skinned, a position that would produce some stretching. Stejneger (1895, p. 436) listed two specimens killed in Florida that measured 8 feet 5 inches (2,565 mm.), and 8 feet 9 inches (2,667 mm.), respectively. Dr. Stejneger did not have access to either of these specimens, nor is it believed that he was able to ascertain the methods of measurement used, thus making the records subject to some doubt. Ditmars (1907, p. 447) reported that the largest specimen he had measured was 8 feet 3 inches (2,515 mm.) long. Later (1931, p. 112) he reported specimens 8 feet 4 inches (2,540 mm.), and 8 feet 6 inches (2,591 mm.).

V. (1913, p. 499) said that he had seen one 7½ feet (2,286 mm.) long in the round, and still longer skins. Ortel (1932, p. 200) records an 8-foot 4-inch (2,540 mm.) specimen.

Rutledge claims several encounters of note; he reports (1938, p. 19) having seen an eastern diamondback 8 feet 1 inch long (2,464 mm.); he killed one measuring 7 feet 9 inches (2,311 mm.) that weighed 34 pounds and had 18 rattles, and a neighbor had killed an 8-footer (1946, p. 225). He writes further (1949, p. 82): "I have carefully measured a diamondback that was 8 feet 11 inches (2,718 mm.) long after his huge head had been shot away. Of course, he was something of a record." Breland (1948, p. 213) mentions 8-foot 6-inch (2,591 mm.), and 8-foot 9-inch (2,667 mm.) specimens, no doubt based on some of the prior records I have already quoted. But Snyder (1949, p. 4), in surveying the operations of Florida commercial dealers, gives the record as 7 feet 3 inches (2,210 mm.). Telford (1952, p. 183) reported a 7-foot 3-inch snake, 15 inches in circumference, taken near Eagle Lake, Polk County, Florida.

While not qualifying for the 7-foot limit, the record of Olds (1910, p. 292), who mentions a 6-foot 11-inch (2,108 mm.) snake from North Carolina, is worthy of remark as being the largest specimen reported from outside Florida, if we neglect the one 8 feet 4 inches (2,540 mm.), weighing 40 pounds, said to have been killed by two boys in the Big Santee Swamp of South Carolina (Wallace, 1950, p. 116). Other details of this story do not encourage belief in its accuracy. Another large diamondback from outside Florida was said to have been found near Beaumont, Mississippi. It was 5 feet 11 inches long, and weighed 31 pounds, several times what a snake of this length would be expected to weigh.

Murrill (1932, p. 128) says that, during the Mediterranean fruit-fly eradication campaign in Florida, between six and eight thousand eastern diamondbacks were killed. Of these, only one approached 8 feet (2,438 mm.) in length. There is certainly no basis whatever for the statement of Curran (1935, p. 335) that 9-foot (2,743 mm.) specimens of *adamanteus* are not rare.

I can add no firsthand information to this discussion of record-breaking specimens of *adamanteus*. The most pertinent observation from my correspondents is contained in a letter received some 25 years ago:

Ft. Myers, Florida, October 27, 1927. Today has been one worth entering. We burned hammocks for several hours during the heat of the day on what is locally known as the Arcadian Prairie. This locality lies between Arcadia and Ft. Myers. We got four king snakes, 10 diamond rattlers, 3 pigmy rattlers, and 1 four-line chicken snake. With much difficulty we measured one large rattler. It seemed to be outstanding among its average 4½- and 5-foot brothers. After several checks we found this massive specimen to be within an inch (one way or the other) of 7 feet 10 inches; from the point of the head to the back, 3¾ inches; circumference at the middle of the body (abnormal due to rage), 17¼ inches. Length of tail, including the broken rattle of 8 segments, 11 inches. These measurements might vary a quarter of an inch, but we feel that they are very nearly correct due to the pains and trouble to check our data twice. This specimen was sold to a snake farm at Boynton, Florida.

In the several hundred specimens of the above species that I have handled, I found that the average is about 4½ to 5 feet in length. Large adults are generally around 6 to 6¼ feet in length. It seems that the head and fangs of the latter are more than proportionately larger. For some strange reason, snakes smaller than four feet in length are not found so often.

*J. S. C. Boswell, Alexandria, Va.*

Reviewing all of these statistics concerning the maximum size attained by this largest of rattlesnakes, I should guess that very rarely the eastern diamondback does measure 8 feet (2,438 mm.), give or take an inch or so. Certain theoretical calculations may be made with regard to the frequency with which unusually large individuals of any species may be expected to occur. I have touched on such calculations elsewhere (1937, p. 23; see also p. 296). Applying similar assumptions to *adamanteus*, namely, that the dispersion curve is normal, the coefficient of variability 15 per cent, and that the average fully adult male *adamanteus* measures 5 feet (1,524 mm.), we find that one specimen out of every 263 adult males should have a length of 7 feet (2,134 mm.), and one specimen in about 31,000 a length of 8 feet (2,438 mm.). Of course, there is no real proof yet available that the frequency of occurrence of exceptionally large individuals follows the normal probability curve, so that these conclusions are to be deemed highly speculative.

*Western Diamondback.*—The western diamond rattlesnake (*C. atrox*), especially in some parts of Texas and Oklahoma, is a large rattlesnake, probably second only to the eastern diamondback (*C. adamanteus*) in size. I have seen some large specimens, certainly exceeding 6 feet (1,829 mm.) in length, but as they were alive they could not be measured either safely or accurately.

Concerning this species, W. A. King, Jr., of Brownsville, Texas, one of the largest commercial snake dealers in the Southwest, wrote me on March 8, 1937:

Checking through my records I find that specimen No. J-6223 received at our farm on July 6, 1926, measured 7 feet 5 inches, exclusive of the rattle. Its circumference was 15.2 inches, weight 24 pounds. Without a doubt this is the largest western diamondback ever captured, and considering the fact that we have been in business for more than 34 years and in that time have never encountered a larger specimen, it may be reasonably assumed that this species never measures over 8 feet in length. The average of the larger specimens varies from 6 feet 4 inches, to 6 feet 10 inches.

More recently (March 10, 1950) Mr. King wrote:

During the spring of 1948 we measured a *C. atrox* at 7 feet 8 inches, excluding the rattle. This is only 3 inches longer than the previous record; however, he was larger. We firmly believe that the average of the *C. atrox* collected in our particular area runs larger than the eastern diamondback. Specimens over 6 feet long are common, so to speak; and others nearing 7 feet are not unusual. While we no longer keep an accurate record of lengths, we do record the larger specimens, and had over 50 collected last year in excess of 6 feet, and 12 that were 7 feet long.

J. D. Mitchell (1903, p. 39) reported that the largest specimens he had seen in Texas measured, respectively, 2, 9, 10, and 11 inches over 6 feet (1,871, 2,057, 2,083, 2,108 mm.). Motl (1936, p. 2) wrote that he had caught many 7-footers in west Texas; as a boy he had seen them up to 8 and 8½ feet (2,438 and 2,591 mm.). But his heaviest rattler weighed only 8½ pounds—much too light for any rattler of the lengths mentioned. A 6-foot rattler would weigh this much, a 7-footer nearly twice as much. From this we may conclude that Motl's more easily ascertained weight data were probably more accurate than the lengths, which were no doubt estimates.

Moore (1930, p. 92) saw a western diamond measuring 7 feet 2 inches (2,184 mm.) in Atoka County, Oklahoma, and another 8 feet 2 inches (2,489 mm.) (after the head had been shot off) near McAlester in the same state. Lane (1946, p. 20) records

one 7½ feet long (2,286 mm.) in the Deep Fork River bottoms in Oklahoma. The *American Guide Series: Texas* (1940, p. 28) says that the western diamond attains a length of 9 feet (2,743 mm.) in that state, a figure wholly without verification.

Curtis (1949, p. 13) mentions two western diamonds collected by Dr. Ira E. Nash as having lengths of 7 feet ½ inch, and 7 feet 8 inches (2,159 and 2,337 mm.), respectively; these were taken near Cedar Hill, Dallas County, Texas. In answer to an inquiry, Mr. Curtis advised me that the snakes were placed in captivity and were measured after death. It is stated that the snakes were not stretched, and that the measurements were made from the tip of the nose to the base of the rattle.

The late S. H. Walker collected western diamonds in the sandy areas of the Coachella Valley in Riverside County, California, over a number of years, taking in excess of 7,000. The maximum length recorded was 5 feet 7 inches (1,702 mm.). This is not to be taken as a reflection on the Texas and Oklahoma reports, since it is well known that *atrox* grows to a larger size in the eastern part of its range. Polaski and Polaski (1952, p. 139), in describing the annual rattler roundup at Waynoka, Oklahoma, said that the largest specimen among 4,000 measured 5 feet 8 inches (1,727 mm.). But prior drives may have disposed of the largest rattlers occurring there. It has been rumored that the recent record-breakers have been planted importations from Texas.

In *Texas Game and Fish*, July, 1954, W. G. McMillan, of Lubbock, Texas, offered \$5.00 per inch for each inch by which a Texas rattler, delivered to him in good condition, might exceed 6 feet in length. The offer was repeated in 1955 (*Texas Game and Fish*, March, p. 30). Later (May, 1955, p. 31) Mr. McMillan reported that two prize winners had been submitted; they were 6 feet 4 inches and 6 feet 9 inches in length.

Altogether, the evidence indicates that the western diamond in the eastern part of its habitat may, in rare instances, attain a length of a few inches over 7 feet (2,134 mm.). But I cannot claim to have measured one of this size.

*Central American Rattlesnakes and Relatives.*—The Central American rattler (*C. d. durissus*) is one of the largest of rattlesnakes, but whether it ever exceeds a length of 6 feet (1,829 mm.) is not definitely known. March (1928, p. 60) reported that the longest in his experience measured slightly less than 6 feet. The South American rattler (*C. d. terrificus*) is shorter, although Machado (1945, p. 50) quotes Ihering to the effect that they reach 1,800 mm. (5 feet 11 inches) in Brazil. The type specimen of Humboldt's *C. loeflingii* from Venezuela was said to measure 1,720 mm. (5 feet 8 inches). Stedman's claim (1796, p. 195) that these snakes reach 8 to 9 feet (2,438 to 2,743 mm.) in Surinam is no doubt fanciful.

A related species, the Mexican west-coast rattler (*C. b. basiliscus*) reaches 6 feet or slightly more. Three very large and heavy individuals of this species were born and raised in the San Diego Zoo. One, a female, attained a length of 6 feet 8½ inches (2,045 mm.) and a weight of 17 pounds at the age of 5 years. Another, a male, measured 6 feet 7½ inches (2,019 mm.) and weighed 15 pounds 14 ounces at the age of 10 years. The third did not quite reach 6 feet (1,829 mm.). All three became exceedingly obese. Knowing the considerable effect that captivity has on the life and growth of rattlesnakes, we cannot be sure that *C. b. basiliscus* attains a length of 6 feet in the wild, although it probably does.

*Canebrake and Timber Rattlesnakes.*—There seems little doubt that the canebrake rattlesnake (*C. h. atricaudatus*) occasionally attains a length slightly in excess of 6 feet (1,829 mm.). In 1937 Percy Viosca of New Orleans wrote me:

The largest canebrake rattlesnake that I recall measuring was 6 feet 2 inches. We get persistent reports of rattlesnakes over 8 feet long, but unfortunately I have never been able to verify any of them. I have a photograph of an 8-foot skin, but this probably means a 6-foot snake.

In 1950 Mr. Viosca advised me that no larger specimen than the one above mentioned had come to hand since the previous report.

The late E. A. McIlhenny, of Avery Island, Louisiana, wrote me in 1945 that he had just measured two of the largest specimens of this subspecies that he had ever seen; they were 6 feet 2 inches, and 6 feet 2½ inches (1,880 and 1,892 mm.). He stated that the measurements were to the base of the rattles. Gowanloch (1943, p. 53) mentions a specimen 6½ feet (1,981 mm.) long. Andre Trawick of the Lakeshore area claimed to have killed one measuring 6 feet 10½ inches (2,096 mm.); this information was received through Mr. Viosca.

The northern subspecies, the timber rattlesnake (*C. h. horridus*), sometimes reaches almost as great a length as its southern relative, the canebrake. Bryan (1879, p. 322) mentioned a New Jersey specimen 6 feet 2 inches (1,880 mm.) in length; and Ditmars (1931, p. 114) reported one of the same length from Massachusetts.

*Miscellaneous Species.*—Aside from the kinds previously listed, I doubt whether any other subspecies of rattlesnake attains a length exceeding 6 feet (1,829 mm.). As a boy in San Diego County more than 50 years ago, I thought that 6-foot red diamond rattlers (*C. r. ruber*) were rather common. But this, it has since turned out, was merely an unfounded opinion, for actual measurements of the largest specimens that have been brought to the San Diego Zoo during the past 30 years have failed to disclose any exceeding 5 feet (1,524 mm.) by more than an inch or so. And there are plenty of primitive areas in this county and below the boundary line in Baja California, where such a monster might grow undisturbed. Sibley (1951, p. 47) mentions a *ruber* 6 feet 3 inches (1,905 mm.), but this requires confirmation with respect to identification and method of measurement. I doubt whether the San Lucan diamondback (*C. r. lucasensis*) grows quite so large as *ruber*.

Although specimens of the various subspecies of *Crotalus viridis*, including the prairie rattler (*C. v. viridis*), the Great Basin rattler (*C. v. lutosus*), the northern Pacific rattler (*C. v. oreganus*), and the southern Pacific rattler (*C. v. helleri*), are frequently said to attain a length of 6 feet (e.g., *American Guide Series: Idaho*, 1937, p. 130), I doubt whether they ever exceed 5 feet by more than one or two inches, and even this length is quite exceptional.

Carlander and Moorman (1951, p. 105) mention a *C. v. viridis* 6 feet 2 inches (1,880 mm.) long, but this certainly requires confirmation. A. M. Jackley informed me that, among the thousands of prairie rattlers killed by him in South Dakota, the longest measured 52 inches (1,321 mm.). I have one reliable record of 57 inches (1,448 mm.).

The maximum record for a Great Basin rattler (*C. v. lutosus*) that I consider reliable was of one 53 inches (1,346 mm.) long reported by S. G. Jewett. I have had reports of specimens of the northern Pacific (*C. v. oreganus*) from A. C. Mackie of

5 feet 4 inches (1,626 mm.), collected near Penticton, British Columbia; and one from C. G. Thompson of 5 feet 2 inches (1,575 mm.), taken near Yosemite Valley, California.

Elsewhere (p. 305) I have discussed the relationship between length and weight in rattlesnakes. It has been indicated that a 7-foot rattler would weigh about 15 pounds, and an 8-footer about 23 pounds. The heaviest rattler of which I have heard was the 7-foot 5-inch western diamond reported by W. A. King, Jr., which was said to have weighed 24 pounds. Rattlesnakes, while by no means the longest venomous snakes—the king cobra, attaining a length of at least 18 feet, holds this distinction—probably attain a greater weight than any other venomous snake, although no doubt closely approached by some of the thick-bodied vipers of Africa.

#### PREHISTORIC RATTLESNAKES

Brattstrom (1954b, pp. 35–36) has described two extinct kinds of rattlesnakes that he believes to have been larger than any existing species, basing this conclusion on a comparison of the size of their vertebrae with those of existing rattlesnakes. One that he has named *Crotalus giganteus* may have reached a length of 12 feet; the other, *C. adamanteus pleistofloridensis*, a probable ancestor of the existing eastern diamondback, is presumed to have been 9 or 10 feet long. The fossils, from which these forms were described, were found in Florida, and are of the Pleistocene, or glacial, epoch. The evidence of these large rattlers of a bygone age does not in any way validate the stories of huge rattlers existing today.

### BODY PROPORTIONS

#### BULK

Rattlesnakes are heavy-bodied, that is, they are thick in proportion to length, when compared with most snakes. Yet they are by no means outstanding in this respect, for some African vipers are proportionately much thicker, to say nothing of some boas and pythons. The thickness of a snake's body, whether in terms of diameter or circumference, does not lend itself to accurate measurement. A live snake can swell its body with an intake of air, and can flatten it as well; and a dead snake is affected by the position and the diameter of the coil in which it has been allowed to set in preservative. For these reasons the length-weight relationship is a better criterion of bulk than the correlation of length with the diameter at mid-body.

The length-weight relationship has been discussed elsewhere (p. 337). It has been shown that female rattlers are heavier-bodied than males of the same length, and that adults are proportionately thicker than young. It has likewise been determined (Klauber, 1937, p. 42) that there are species differences, for the southern Pacific rattler (*C. v. helleri*), the southwestern speckled rattler (*C. m. pyrrhus*), and notably the sidewinder (*C. cerastes*), are stouter-bodied than the prairie rattlesnake (*C. v. viridis*). Much remains to be done in establishing species differences in bulk; for individual differences, caused by success in obtaining food, the season of the year, and the breeding condition of females, are so extensive that the measurements and weights of large numbers of snakes at all stages of growth must be available if dependable averages are to be obtained.

## HEAD DIMENSIONS

The head sizes of rattlesnakes, in proportion to the lengths of their bodies, differ considerably among the several species, some kinds having conspicuously large heads and others small, compared with the generic average. These differences are of some value in segregating species and determining their relationships. They are also of some practical importance, since large-headed species tend to have longer fangs and more venom, and therefore are likely to be the more dangerous.

Some years ago (Klauber, 1938) I made a rather detailed study of rattlesnake head-length proportionalities, with the particular object of determining specific, ontogenetic, sexual, and individual differences. The following outline summarizes the results set forth in that study, to which readers seeking greater detail may refer. However, to the extent that head ratios are included in the tables that follow, they are to be considered as superseding those in the 1938 presentation, since they are based on enlarged collections.

In the course of preservation, some shrinkage of the head, disproportionate to the shrinkage of the body, was disclosed, an average head reduction of 6.8 per cent being evident, while the body shrank only 2 per cent. For this reason the head length should, where possible, be determined prior to preservation. This can best be done just after the snake has been killed and is still soft, for measurements of live specimens cannot be made with accuracy, and they involve some danger as well. The head length is taken as the distance from the tip of the snout—the vertical face of the rostral scale—to the posterior end of either mandible.

Sexual dimorphism was first investigated. No consistent difference was disclosed between the males and females with respect to the ratio of their head lengths to lengths over-all, except in case of the sidewinder (*C. cerastes*). In this species the female was found to have a proportionately larger head. This rattlesnake species is also peculiar in being the only one in which the female grows to a larger size than the male. As has been shown in the prior paper (p. 36), these two deviations from the rattlesnake normal are probably interrelated.

In investigating a character such as head length, which obviously changes with body growth, the problem is to determine the nature of the correlation between head and body, whether represented by a linear equation or one of higher degree, and how closely the individuals adhere to the regression line representing the mean of the group. In the present instance the relationship was found to be substantially linear in every subspecies investigated. A graphic representation of the relationship in one subspecies, the red diamond rattler (*C. r. ruber*), is shown in figure 4:1. A straight-line regression of this type can be expressed algebraically by an equation of the form  $H = aL + b$ , where  $H$  is the head length at any over-all length  $L$ , and  $a$  and  $b$  are constants which, however, differ for each subspecies. The lengths are expressed in millimeters.

In the case of the *ruber* line shown in figure 4:1, the equation is  $H = 0.0385L + 8.0$ .<sup>1</sup> Using this equation one may determine, for example, that a young *ruber* having a body length of 300 mm. would have a head length of 19.55 mm., and an adult 1,300 mm. long would have a head length of 58.05 mm. It should be under-

<sup>1</sup> This differs somewhat from the equation given in the table that follows. The regression line in figure 4:1 was based on 100 specimens of *ruber*, whereas the coefficients listed in the table were determined from the measurements of several hundred heads.

stood that, in citing figures to one one-hundredth of a millimeter, I am not suggesting that the heads can be measured to any such degree of accuracy, or that the formula itself warrants an expression of head-length averages to one one-hundredth of a millimeter. These figures are given only so that the reader may check the use of the formula. It would be more practical to state that a 300-mm. *ruber* has a head length of about 19½ mm., and a 1,300-mm. snake one of about 58 mm. These are only average figures; individual snakes will fall above or below the average, the extent of the dispersion being indicated by the small circles representing individual snakes in the *ruber* example portrayed in figure 4:1.

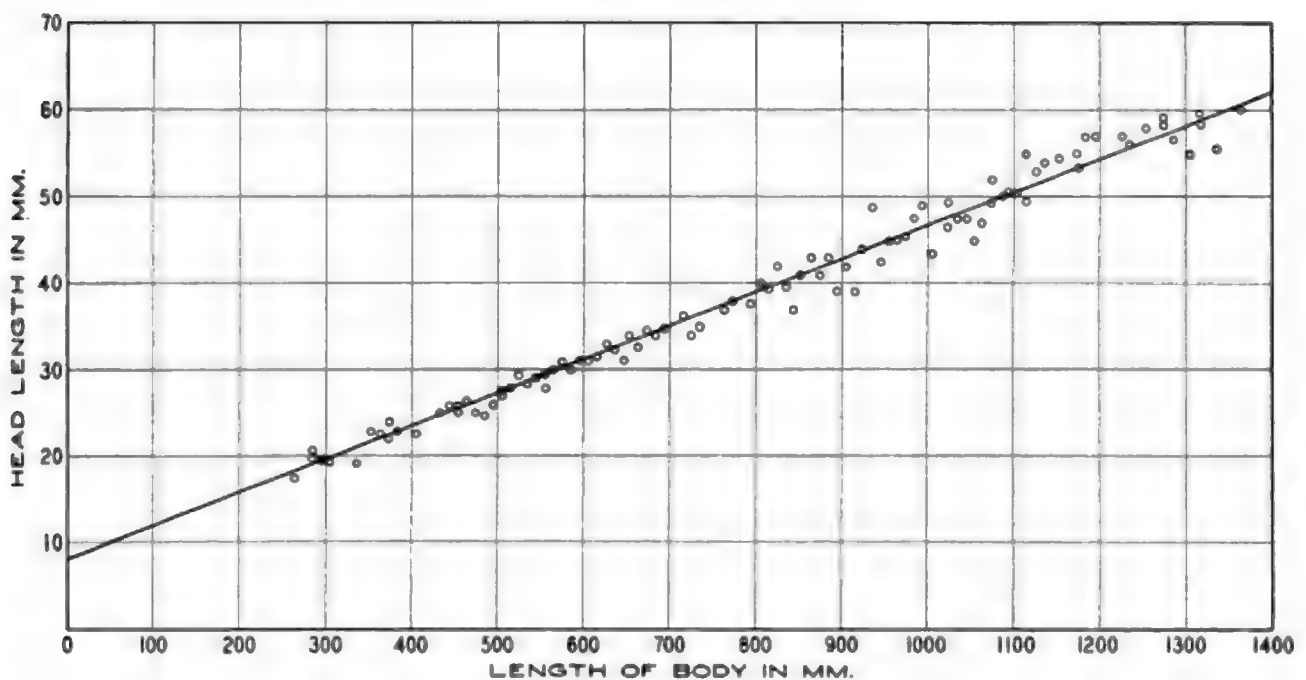


Fig. 4:1. Relationship between the length of the head and of the body (over-all) in 100 red diamond rattlesnakes (*C. r. ruber*).

The other species and subspecies of rattlesnakes have been investigated by the use of diagrams similar to that shown for *C. r. ruber*, and straight-line equations of the form  $H = aL + b$  have been deduced for all subspecies of which sufficient specimens were available to afford fairly reliable trend lines. The results are set forth in table 4:2. The invariable presence of the positive term  $b$  in these head-length equations indicates that young rattlers have proportionately larger heads than adults, a common condition among animals. For example, taking the 300-mm. (young) and 1,300-mm. (adult) red diamonds, we find that the juvenile has a head comprising 6½ per cent of its length over-all, whereas in the adult the head length is only 4½ per cent.

There are those who object to a straight-line formula, such as that disclosed, for a relationship of this type, for it is clear that the formula cannot be valid during the prenatal stage, since, theoretically, a snake of no body length at all would have a head equal to the length  $b$ . Curves of the parabolic type  $H = cL^2$  are found to be accurate representations of many relationships involving relative growth and body-part proportionality, and such curves are theoretically preferable to straight lines since they pass through the origin; thus a creature of zero body length would have a head of zero length. But, in the present study, it was found that linear equations

of the type first discussed fit the actual head-body variations from juvenile to adult stage even better than those of the parabolic type, and have the additional advantage of simplicity in both derivation and use. It is to be admitted that, in several subspecies, the equation gives a figure for the head length, at about half growth, slightly below a true figure. Elsewhere (1948, p. 8) I have set forth the coefficients and exponents of the parabolic equations representing the head-length proportionality of a number of series of rattlers of different kinds, but I do not consider these determinations of sufficient practical use to be reproduced in the present summary.

With regard to the dispersion of individuals about the straight lines of best fit, it was found in the earlier study that, ontogenetically, the dispersion is nearly uniform on a percentage basis, but increases slightly in the adult stage, as compared with the juvenile. The coefficient of variation of head length about the head-body regression line was found to vary from about  $2\frac{1}{2}$  to  $3\frac{1}{2}$  per cent. The distribution is substantially normal.

With this type of dispersion, it is possible to use head-length as a diagnostic character, that is, in differentiating two species or subspecies. It is first necessary to compute the probable head-length of each specimen of the two series to be compared, at some standard length over-all, and then to determine the significance of the difference between the two series. Examples of this method are set forth in the prior paper (Klauber, 1938, p. 20); also, the general use of body parts, whose proportionalities vary ontogenetically, to determine the significance of species or sexual differences, has been further discussed in other connections (Klauber, 1943a, pp. 40, 46; 1945, p. 70). I have also treated elsewhere (1938, p. 29) the relationship between dwarfed forms and their prototypes, and have reached the conclusion that the adults of the two forms—the dwarf and its prototype—tend to have the same head proportionality at corresponding ages rather than at similar body sizes.

In the former discussion (1938, p. 39) I summarized the differences evident between the various species of rattlesnakes. Some of these differences are quite conspicuous, for some species deviate materially from the rattlesnake mode. For example, the tiger rattler (*C. tigris*) and the San Lucan speckled rattler (*C. m. mitchelli*) have notably small heads; whereas those of the Mexican blacktail (*C. m. nigrescens*) and the eastern diamondback (*C. adamanteus*) are outstandingly large. To summarize these differences in head proportionality, the head-length trend-line equations of most rattlesnake subspecies—those of which adequate specimens are available—are set forth in table 4:2; also, there are presented the head lengths at birth and at the standard size designated as a large male (for each subspecies), as well as the number of times the head is contained in the length over-all at birth and at full growth (as represented by large males). This latter method of stating head-length proportionality is somewhat easier to visualize than its reciprocal—the head length as a percentage of the body length. The marked differences between the figures in the final two columns of table 4:2 should readily convince anyone of the important inaccuracy resulting from averaging head-length proportionalities regardless of age—as is not infrequently seen in taxonomic studies.

It is of interest to determine the nature of the generic trend in rattlesnake head sizes by means of a scatter diagram, in which each subspecies is represented by a

TABLE 4:2  
CORRELATION OF HEAD LENGTH (*H*) WITH BODY LENGTH (*L*)  
Equation: *H* = *aL* + *b*. All dimensions in millimeters

Subspecies	<i>a</i>	<i>b</i>	Values of <i>H</i>		Values of <i>L/H</i>	
			At birth	Of large males	At birth	Of large males
<i>C. adamanteus</i> .....	0.0415	9.4	23.9	86.2	14.6	21.5
<i>C. atrox</i> .....	0.0351	8.7	20.3	68.4	16.2	24.9
<i>C. basiliscus basiliscus</i> .....	0.0333	9.7	20.7	66.3	16.0	25.6
<i>C. cerastes cerastes</i> .....	0.0368	5.8	12.2	26.0	14.3	21.2
<i>cercobombus</i> .....	0.0381	5.5	12.5	28.4	14.8	21.1
<i>laterorepens</i> .....	0.0378	6.0	13.2	30.2	14.4	21.2
<i>C. durissus durissus</i> .....	0.0302	12.1	21.6	60.4	14.6	26.5
<i>culminatus</i> .....	0.0365	10.4	21.9	68.8	14.4	23.2
<i>terrificus</i> .....	0.0351	9.2	19.9	58.3	15.3	24.0
<i>totonacus</i> .....	0.0333	9.2	19.7	62.4	16.0	25.6
<i>tzabcan</i> .....	0.0368	9.2	20.8	68.1	15.1	23.5
<i>C. enyo enyo</i> .....	0.0304	7.5	14.3	33.3	15.7	25.5
<i>cerralrensis</i> .....	.....	.....	.....	.....	.....	30.0
<i>C. exsul</i> .....	0.0354	8.2	16.7	40.1	14.4	22.4
<i>C. horridus horridus</i> .....	0.0324	9.1	18.3	49.6	15.6	25.2
<i>atricaudatus</i> .....	0.0328	9.2	19.0	56.8	15.8	25.5
<i>C. intermedius intermedius</i> .....	0.0327	6.1	11.0	22.5	13.6	22.2
<i>omiltemanus</i> .....	0.0337	5.9	11.3	24.4	14.2	22.5
<i>C. lepidus lepidus</i> .....	0.0350	6.3	13.0	29.1	14.6	22.3
<i>klauberi</i> .....	0.0345	6.6	13.3	29.7	14.7	22.6
<i>morulus</i> .....	0.0344	7.1	13.6	29.4	14.0	22.1
<i>C. mitchelli mitchelli</i> .....	0.0286	7.9	14.8	34.8	16.2	27.0
<i>muertensis</i> .....	0.0353	6.6	13.1	28.5	14.1	21.8
<i>pyrrhus</i> .....	0.0371	7.0	16.8	47.8	15.8	23.0
<i>stephensi</i> .....	0.0324	7.6	15.1	35.8	15.2	24.3
<i>C. molossus molossus</i> .....	0.0398	6.8	17.9	54.8	15.6	21.9
<i>nigrescens</i> .....	0.0405	8.8	19.7	55.4	13.7	20.8
<i>C. polystictus</i> .....	0.0367	6.4	14.8	37.6	15.5	22.6
<i>C. pricei pricei</i> .....	0.0395	5.0	11.3	26.7	14.2	20.6
<i>C. pusillus</i> .....	0.0442	3.8	11.5	31.2	15.2	19.9
<i>C. ruber ruber</i> .....	0.0374	8.4	19.6	60.8	15.3	23.0
<i>lucasensis</i> .....	0.0375	8.9	19.8	57.7	14.6	22.5
<i>C. scutulatus scutulatus</i> .....	0.0316	8.7	17.1	43.5	15.5	25.3
<i>salvini</i> .....	.....	.....	.....	.....	.....	21.2
<i>C. stejnegeri</i> .....	0.0300	9.0	14.1	27.0	12.1	22.2
<i>C. tigris</i> .....	0.0254	8.9	14.2	28.5	14.8	27.0
<i>C. tortugensis</i> .....	0.0315	8.1	16.0	39.6	15.6	25.3
<i>C. triseriatus triseriatus</i> .....	0.0421	5.8	13.2	31.9	13.3	19.4
<i>aquilus</i> .....	0.0360	7.2	13.5	29.5	13.0	21.0
<i>C. unicolor</i> .....	0.0340	9.0	17.0	41.3	13.8	23.0
<i>C. viridis viridis</i> .....	0.0345	7.7	17.0	51.5	15.9	22.3
<i>abyssus</i> .....	0.0330	8.0	16.3	41.0	15.3	24.4
<i>caliginis</i> .....	0.0367	7.4	14.4	31.3	13.2	20.8
<i>cerberus</i> .....	0.0353	7.5	16.5	44.6	15.4	23.5
<i>decolor</i> .....	0.0309	7.5	13.8	30.7	14.9	24.4
<i>helleri</i> .....	0.0361	8.2	18.1	51.5	15.2	23.3
<i>lutosus</i> .....	0.0337	7.5	16.4	46.3	16.2	24.8

TABLE 4:2—Continued

Subspecies	a	b	Values of <i>H</i>		Values of <i>L/H</i>	
			At birth	Of large males	At birth	Of large males
<i>C. viridis</i> —Continued						
<i>nuntius</i> .....	0.0324	7.3	13.1	28.4	13.7	22.9
<i>oreganus</i> .....	0.0339	7.6	16.8	46.6	16.1	24.7
<i>C. willardi willardi</i> .....	0.0388	6.8	13.2	28.5	12.5	19.6
<i>meridionalis</i> .....						19.3
<i>silus</i> .....	0.0388	6.2	12.8	29.1	13.3	20.3
<i>S. catenatus catenatus</i> .....	0.0302	9.3	15.9	35.0	13.8	24.3
<i>tergeminus</i> .....	0.0340	8.1	15.4	35.3	14.0	22.7
<i>S. miliarius miliarius</i> .....	0.0343	7.0	12.5	25.2	12.8	21.0
<i>barbouri</i> .....	0.0356	6.5	12.6	28.9	13.5	21.8
<i>streckeri</i> .....	0.0357	7.1	13.0	29.6	12.7	21.3
<i>S. ravus</i> .....	0.0388	6.8	13.6	30.9	12.9	20.1

single point, as located by the average head size of a large male of that subspecies plotted against the corresponding length of body of a large male—that is, using the figures in column 4 of table 4:1 and column 4 of table 4:2 as co-ordinates. It is found that the relationship is closely represented by the equation  $H = 37.5L + 5$ , where  $H$  is expressed in millimeters and  $L$  in meters. The constant term indicates that the generic trend is similar to the ontogenetic trend within subspecies, namely, smaller subspecies tend to have larger heads, relatively speaking, than the large subspecies. Another useful generic scatter diagram is that in which  $L/H$  is plotted against  $L$ . This has the advantage of accentuating the deviations of individual subspecies from the generic norm. For, one cannot compare adult head proportionalities, as shown in the final column of table 4:2, without taking into consideration the normal generic tendency of smaller rattlers to have proportionately larger heads than their larger relatives.

It is found, from this study of departures from the generic norm, that the rattlesnakes with unusually large heads are, among the smaller kinds, *willardi* and its subspecies, *triseriatus triseriatus*, *pusillus*, and *ravus*; *nigrescens* is large-headed among the medium-sized subspecies, and *adamanteus* among the large. Those with abnormally small heads are *omiltemanus*, *intermedius*, and *nuntius* among the small subspecies; and *enyo*, *cerralvensis*, *tigris*, and *mitchelli* among the medium-sized. The last two are outstanding in their deviation from the generic trend line. No large rattlesnakes have exceptionally small heads.

Head widths were also investigated, although it was found that width measurements could not be made with the same accuracy as those of length. It was learned that adult rattlers have wider heads, proportionately, than juveniles. The coefficient of variation of width about the width-length regression line is about 5 per cent. Most rattlesnakes have a head-width to head-length ratio of about 62 to 72 per cent at birth; and 74 to 83 per cent at maturity. The Mexican lance-headed rattler (*C. polystictus*) and the Lower California rattler (*C. enyo*) are notable for their narrow heads, whereas the speckled rattlers (*C. mitchelli*) and sidewinders (*C. cerastes*) are characterized by wide heads. As to head depth, narrow-headed rattlers

tend to have deep heads compared to their widths, and wide-headed rattlers—notably the southwestern speckled rattler (*C. m. pyrrhus*)—have especially shallow heads.

#### TAIL DIMENSIONS

Rattlesnakes have relatively short tails. In most snakes, the tail, aside from being the repository of the scent glands, and the retracted hemipenes in the male, is used primarily as an aid to locomotion, and in some snakes for holding and climbing. But in the rattlesnakes the tail is foreshortened by the attachment of the rattle, and concurrently serves principally as a muscular rattle-vibrator. Rattlesnakes exhibit some species difference in tail length, when they are compared in terms of the ratio of the length of the tail to the length of the snake over-all. In determining the tail length, the measurement is made from the center of the anal plate to the anterior edge of the proximal rattle.

Nearly all snakes exhibit a considerable sexual dimorphism in tail length, and ontogenetic differences are also manifest. These differences have been investigated in a previous study (Klauber, 1943a), wherein ontogenetical changes were set forth in table 9, and sexual dimorphism in tables 14 to 16. It was found that the tail proportionality changes considerably with age; it is usual, although not universal, for the ratio of the tail to the length of the snake over-all to increase with age. This is particularly evident in the males. Slim snakes tend to have proportionately longer tails. The rattlers, being heavy-bodied or thick snakes, would be expected to have short tails, even were they not abnormally shortened by the attachment of the rattles. Their nearest relatives, the pit vipers of the genera *Agkistrodon* and *Bothrops*, are short-tailed.

Sexual dimorphism is higher in short- than in long-tailed genera; it is correspondingly high among the rattlesnakes. On the contrary, however, ontogenetic change, that is, a change in proportionate tail length as a snake grows, is found to be less in the rattlesnakes than in most other snakes. In fact, it can virtually be ignored in the males, although of some importance in the females, whose tails become proportionately shorter as the snakes age. The tails of the males, on the other hand, to the small extent that they change as the snake grows, tend to become slightly longer in proportion to the length of the snake over-all. The sidewinders are exceptional, in that both sexes have proportionately longer tails when adults, the males to a greater extent than the females.

As was the case with head proportionality, it is found that the variation in the tail-length ratio that takes place as a snake ages, may be expressed by a straight-line equation, although in this case it is necessary to treat the sexes separately (Klauber, 1943a, p. 52). The variation of the individual specimens about the regression line is found to be higher than in the head studies, such variations usually running from 6 to 9 per cent. The percentage of variation, that is, of the dispersion about the regression line, tends to be constant throughout life.

Because of the relatively slight ontogenetic variation in the rattlesnakes, it is feasible to neglect such changes in taxonomic studies, except in the most exacting problems, or where one of the series to be compared is composed predominately of juveniles and the other of adults. On the average, it was found that male tail-ratios increase about 1½ per cent as the snakes grow from youth to age, whereas the

females correspondingly decline by  $4\frac{1}{2}$  per cent. Data on the regression lines of 52 different series of rattlers will be found in the previous paper (Klauber, 1943a, table 19). A few of the lines representing Mexican species have now been amended, based on new material. The new equations are set forth under the several subspecies in another paper (Klauber, 1952, pp. 7, 21, 26, 36, 41, 49, 54, 62, 68, 73, 77, 80, 92, 97, 105, 107, 111, and 113).

Although it is usually proper to ignore ontogenetic variation, sexual differences in tail proportionality can never be neglected in taxonomic problems involving rattlesnakes, for the tails of the males are longer than those of the females to an important degree, varying from a minimum of about 16 per cent (of the female length) in the pigmy rattlesnakes (*Sistrurus miliarius*) and 19 per cent in the southwestern speckled rattler (*C. m. pyrrhus*), to as high as 45 to 52 per cent in some subspecies of the Neotropical rattlesnake (*C. durissus*), the Lower California rattler (*C. enyo*), and the sidewinder (*C. cerastes*). In most species of rattlers the male tail-length superiority is of the order of 28 to 35 per cent.

With regard to the percentage of over-all length represented by the tail, this, in most species, runs from 7 to 9 per cent in the males, and from 5 to 6.9 per cent in the females. The figures for the adults of such subspecies as are available in adequate numbers to assure reasonable accuracy are presented in table 4:3.

The snakes belonging to the genus *Sistrurus* are long-tailed, especially the pigmy rattlers (*S. miliarius*). The longest-tailed of all rattlers is *C. stejnegeri*; others in this genus with exceptionally long tails are *willardi*, *triseriatus*, *pusillus*, and *durissus* and its allies. The shortest-tailed rattler is the El Muerto Island speckled rattler (*C. mitchelli muertensis*) with a male proportion of 6.7 per cent, and a female of 5.3, followed by the red diamond (*C. r. ruber*) and the Cedros Island diamond (*C. exsul*), with adult male tail percentages of 6.9 and female percentages of about 5.3.

Species of rattlesnakes having long tails usually have relatively small rattles. Thus, the long-tailed rattlesnake (*C. stejnegeri*) has, proportionate to its body length, the smallest rattles of any species of the genus *Crotalus*; and similarly the pigmy rattler (*S. miliarius*) has an elongated tail and small rattle. The Tancitaran dusky rattler (*C. pusillus*) is another species with a long tail and conspicuously small rattles. It is obvious that a long, tapering tail could be terminated only by a relatively small matrix and therefore a small rattle. These species with rattles so small as to be almost inaudible were either primitive, or are evolving in the direction of sacrificing whatever benefit there may be in the rattle, in favor of regaining the crawling assistance inherent in the longer tail. Structural and muscular difficulties no doubt inhibit the attainment of both advantages simultaneously, for a long, tapering tail could neither produce a large rattle at the end, nor vibrate it successfully if it were evolved.

Although the correlation of rattle size with tail length is evident, it is by no means a perfect one. Tail length does not explain the relatively large rattles of the San Lucan speckled rattler (*C. m. mitchelli*) or the tiger rattler (*C. tigris*). The Central American rattler (*C. d. durissus*) and its relatives and the Mexican west-coast rattler (*C. b. basiliscus*) are rather long-tailed. They start life with small buttons, but eventually attain rattles as large as those of any other species.

TABLE 4:3  
TAIL-LENGTH PROPORTIONS OF RATTLESNAKES  
Average Tail Length of Adults, Expressed as a Percentage of Length Over-all

Subspecies	Males	Females
<i>C. adamanteus</i> .....	8.3	6.3
<i>C. atrox</i> .....	7.9	5.8
<i>C. basiliscus basiliscus</i> ..	9.2	6.3
<i>C. cerastes cerastes</i> .....	9.5	6.5
<i>cercobombus</i> .....	8.4	5.7
<i>laterorepens</i> .....	8.6	6.2
<i>C. durissus durissus</i> .....	10.0	6.9
<i>culminatus</i> .....	7.9	6.5
<i>terrificus</i> .....	10.0	6.6
<i>tolonacus</i> .....	8.2	6.5
<i>tzabcan</i> .....	8.8	6.8
<i>C. enyo enyo</i> .....	9.5	6.4
<i>C. exsul</i> .....	6.9	5.4
<i>C. horridus horridus</i> .....	7.7	5.9
<i>atricaudatus</i> .....	7.8	6.2
<i>C. intermedius intermedius</i> .....	8.5	6.6
<i>omiltemanus</i> .....	8.8	6.9
<i>C. lepidus lepidus</i> .....	8.6	7.1
<i>klauberi</i> .....	8.1	6.6
<i>morulus</i> .....	9.0	7.2
<i>C. mitchelli mitchelli</i> .....	8.2	6.4
<i>muertensis</i> .....	6.7	5.3
<i>pyrrhus</i> .....	7.2	6.1
<i>stephensi</i> .....	8.1	6.0
<i>C. molossus molossus</i> .....	7.1	5.7
<i>nigrescens</i> .....	7.7	5.5
<i>C. polystictus</i> .....	7.6	5.9
<i>C. pricei pricei</i> .....	8.0	6.5
<i>C. pusillus</i> .....	10.5	8.6
<i>C. ruber ruber</i> .....	6.9	5.2
<i>lucasensis</i> .....	7.3	5.3
<i>C. scutulatus scutulatus</i> .....	7.4	5.3
<i>salvini</i> .....	7.7	5.5
<i>C. stejnegeri</i> .....	12.7	9.8
<i>C. tigris</i> .....	8.4	6.4
<i>C. tortugensis</i> .....	7.5	5.8
<i>C. triseriatus triseriatus</i> .....	10.4	8.1
<i>aquilus</i> .....	9.3	7.7
<i>C. unicolor</i> .....	10.2	7.1
<i>C. viridis viridis</i> .....	7.5	5.3
<i>abyssus</i> .....	7.3	5.9
<i>caliginis</i> .....	7.9	6.0
<i>cerberus</i> .....	6.9	5.4
<i>decolor</i> .....	7.8	5.9
<i>helleri</i> .....	7.4	5.6
<i>lutosus</i> .....	7.2	5.6
<i>nuntius</i> .....	7.7	5.5
<i>oreganus</i> .....	7.4	5.7

TABLE 4:3—Continued

Subspecies	Males	Females
<i>C. willardi willardi</i> .....	10.2	8.0
<i>meridionalis</i> .....	11.7	9.8
<i>silus</i> .....	11.0	9.1
<i>S. catenatus catenatus</i> .....	10.6	8.1
<i>tergeminus</i> .....	11.0	8.4
<i>S. miliarius miliarius</i> .....	12.0	9.8
<i>barbouri</i> .....	12.3	10.6
<i>streckeri</i> .....	12.7	11.0
<i>S. rarus</i> .....	9.8	7.7

PHYSIOLOGICAL SUMMARY

This book makes no pretense of including a complete anatomical study of the rattlesnake, a project that I should be ill-equipped to undertake. However, certain features of rattlesnake anatomy are discussed with varying degrees of thoroughness in other appropriate chapters, including the rattle in chapter 5, the skin and sense organs in chapter 6, the sex organs in chapter 10, and the biting mechanism, including the venom gland, duct, and fangs, in chapter 11. In the present chapter, I shall mention two phases of snake anatomy that have been seriously affected by the attenuation of the body: first, the longitudinal arrangement of the principal organs; and, second, the lungs and respiration. A few references of interest in connection with subjects that I have not treated are: *osteology*, Taylor, 1895, p. 281; Brattstrom, thesis to appear shortly; *muscles*, Mosauer, 1935, p. 81; Haas, 1952, p. 573; *circulatory system*, Beddard, 1904, p. 331; Brongersma, 1949, p. 57; 1951, p. 3; *blood*, Luck and Keeler, 1929, p. 703; Carmichael and Petcher, 1945, p. 696; Cohen, 1951, p. 6; 1954, p. 98.

PLACEMENT OF ORGANS

As an example of the longitudinal placement of organs, and the lengths of some of them, the data on a large male southwestern speckled rattlesnake ( *C. m. pyrrhus* ), as determined by Charles E. Shaw, are presented in table 4:4. In this table, lengths are given both in millimeters and in percentages of body length. It should be emphasized that the latter means body length exclusive of both head and tail. This snake was 1,077 mm. in over-all length, with a head length of 47 mm., and a tail length of 92 mm.; thus the body length alone—the basic figure for table 4:4—was 938 mm. The elongation of some of the organs, particularly of the lung, liver, and kidneys, is evident from the high percentages of the body length that they occupy.

LUNGS

The attenuated shape of the ophidian body has resulted in a greater modification in the lungs than in any other organ. Whereas some snake families (e.g., the Boidae) have retained two functional lungs (although no longer equal in size), in most

snakes only a single functional lung remains; the other lung, if present at all, is rudimentary and nonfunctional. Two other unusual pulmonary developments are evident in many snakes: first, an increase in the active aerating surface by an alveolar lining along the dorsal-posterior aspect of the trachea; and, second, an enlargement of the air storage capacity of the lung by its extension posteriorly in the form of a nonvascular air sac.

Tyson (1683, p. 29), who was the first to make an accurate dissection of a rattlesnake, observed that the lung was very long, that the anterior part lies along the trachea, and that the posterior is only a sort of "bladder," as he called it, without

TABLE 4:4  
PLACEMENT OF ORGANS IN A SOUTHWESTERN SPECKLED RATTLESNAKE (*C. m. pyrrhus*)

Organ	Measurements <sup>a</sup> millimeters			Percentages of body length of 938 mm.		
	Front	End	Net length	Front	End	Net extent
Lung <sup>b</sup> .....	24	733	707	3	78	75
Heart.....	354	388	34	38	42	4
Liver.....	390	514	124	42	55	13
Stomach.....	461	593	132	49	63	14
Stomach (mucosal folds).....	498	579	81	53	62	9
Gall bladder.....	618	632	14	66	67	1
Spleen.....	627	637	10	67	68	1
Kidney, right.....	754	894	150	80	95	15
left.....	788	887	99	84	95	11
Testis, right.....	676	695	19	72	74	2
left.....	733	754	21	78	80	2

<sup>a</sup> Front and end measurements signify the distance of the anterior and posterior points of each organ behind the anterior end of the body, that is, the posterior edge of the head.  
<sup>b</sup> The trachea terminated at 399 mm.; the mid-point of the transition between the alveolar and nonalveolar sections of the lung was at about 423 mm. No boundary was evident between the tracheal and bronchial lung sections.

respiratory cells. Cope (1894a, 1894b), in his search for anatomical characters of snakes that might aid in their classification and differentiation, made some advances in knowledge by pointing out the familial consistency in the morphology of the lungs. Although Cope was by no means the first herpetologist to observe generic differences, the extent of his investigations did much to establish the lungs as having some promise in classification. He was the first to use the term "tracheal lung" for the vascular section along the trachea. He concluded that the active lung retained by snakes with only one lung was the left lung (1894a, p. 218; 1894b, p. 838). Later, this was shown by Butler (1895, pp. 692, 697) to be in error; others (e.g., Brongersma, 1951, p. 3; Varde, 1951, p. 79) have since confirmed the fact that the right lung is the one that remains functional in the many genera of snakes, including the rattlesnakes, that have only a single active lung.

The parts of the respiratory apparatus of the rattlesnake that I shall briefly mention are the glottis, the trachea, the tracheal (anterior) lung, the central or bronchial lung, the posterior nonvascular sac, and the rudimentary left lung. The glottis is notable in that it may be protruded out of the snake's mouth while food is being swallowed, thus permitting a snake to breathe during a protracted swallowing of prey. Bellairs and Underwood (1951, p. 218) mention the special muscles that

make the protrusion of the glottis possible. The trachea of some snakes is, as in many animals, a tube that is prevented from collapsing by the presence of cartilaginous rings. In the rattlesnakes (as well as in many other kinds of snakes) the upper surface of the posterior trachea has become the site of a complex of respiratory alveoli. This has been effected by the elimination of the upper halves of the usual tracheal rings and by the extension forward, almost to the head, of lung tissue along the dorsal aspect of the trachea. This lung tissue is fed with air directly from the trachea that lies below it, for the trachea is split dorsally from the beginning of the tracheal lung to its entrance into the bronchial lung. This slit in the trachea therefore constitutes the lumen of the tracheal lung; the edge of the slit is slightly serrated by the protrusion of the ends of the interrupted cartilaginous rings.

In some snakes a boundary is evident between the tracheal and bronchial lung sections, but in the rattlesnakes the tracheal lung has become so large and important that it seems to be a forward continuation of the bronchial lung, without a definite boundary being apparent between them (Cope, 1894a, p. 222; Boulenger, 1913, p. 78; Thompson, 1913, p. 423; Noble, 1921, p. 170; Brongersma, 1949, p. 57; 1951, p. 31; Varde, 1951, p. 80; Bellairs and Underwood, 1951, p. 219). Brongersma (1949, p. 57) prefers to consider the tracheal lung as terminating opposite the center of the heart or opposite the lumen of the rudimentary left lung, if one remains, but this is arbitrary. The vascular system serving the lungs has been described by Brongersma (1949, p. 57; 1951, p. 31), who points out that the pulmonary vessels have been much modified by the presence of the tracheal lung and the resulting alveolar concentration anterior to the heart. The histology of the lung has been discussed by Varde (1951, p. 81).

The tracheal lung must not be thought of as a minor addition to the snake's respiratory capacity. As Thompson (1913, p. 423) has pointed out, the alveoli of the tracheal lung are small, thick, and superimposed, whereas those of the bronchial lung are thinner and shallower. "Bronchial" is a convenient designation for the middle section of the lung, but this term should not be assumed to assign a superior function to this section. Evidently the designation stems from the fact that it gets its air supply from the bronchus or terminus of the trachea. Brongersma (1951, p. 6) has pointed out that the trachea, at its caudal end, opens into the lung without the presence of external bronchi. In fact, as the slit trachea is open to the lung above it throughout its length, its terminus retains no particular importance.

Posteriorly the bronchial lung gradually loses its alveolar structure, and the final section of the lung is a bladderlike tube with a thin, translucent wall. This part is merely an air reservoir, without function for blood aeration. Brongersma (1949, p. 57) refers to it as an anangious air sac. Various theories have been proposed to account for this posterior air reservoir. It is obviously of utility for snakes that spend much time in water, since it both increases buoyancy and makes a longer immersion possible. For snakes that are primarily land dwellers, it may be useful during the food-swallowing process, just as is the extended glottis. Or, the posterior inflation of the body, which the air reservoir makes possible, may be beneficial by enhancing the threatening posture of a snake, both by increasing its apparent size and by prolonging the hiss. Rattlers show both these effects.

The tracheal lung extends the aerating tissue, of particular importance in a slim body where space is at a premium. Cope (1894b, p. 839) pointed out that, in a creature like a snake, the sizes of whose meals are very large in proportion to its own size, the longitudinal extension of the lung is of value when one section of the body is distended with food and lung ventilation in that section is thus reduced. Another possible function of the tracheal lung is to enhance inflation of the anterior part of the body, which is a part of the threatening postures of some snakes (Cope, 1894b, p. 839; Noble, 1921, p. 167), although rattlesnakes are not particularly addicted to this. Butler (1895, p. 710) thought that the one-sided displacement of the stomach and the adjacent esophagus had led to the suppression of the left lung and the extension of the right. Thompson (1913, p. 414) evolved the theory that venom production had entailed an enlargement of the liver, which in turn crowded the lung. This caused the forward extension along the trachea, a convenient foundation for the extension of pulmonary tissue when the need arose for increased breathing surface. Bellairs and Underwood (1951, p. 219) favor the theory that food pressure has necessitated an extended lung not susceptible to having all its parts compressed simultaneously during feeding.

The lungs of rattlesnakes indeed occupy a surprisingly large part of the body length of the snake. Richard C. Schwenkmeyer (unpublished manuscript) established the following lung landmarks as percentages of body length (exclusive of head and tail) in *C. r. ruber*: anterior beginning of lung tissue 5 per cent; end of vascular tissue 45 per cent; end of air sac 81 per cent. Thus, the total length of the lung is about 76 per cent of that of the body; and, of this, the vascular part is 40 per cent, and the nonvascular 36 per cent. In a 905-mm. specimen of *ruber*, the lung capacity was found to be 76 cc. These figures may be compared with those in table 4:4 on *C. m. pyrrhus*.

Some rattlesnakes have rudimentary left lungs; in others even this rudiment has disappeared. Cope (1894a, p. 223) found rudimentary lungs present in *C. horridus* and absent in *S. catenatus*, *C. adamanteus*, and *C. viridis*. Butler (1895, p. 708) found a rudimentary left lung in *C. horridus*, but absent in *C. durissus*. Brongersma (1951, p. 3) found a rudimentary left lung in *C. durissus*. Schwenkmeyer (unpublished manuscript) found rudimentary left lungs usually present in *C. b. basiliscus*, *C. durissus*, *C. h. horridus*, and *C. m. molossus*; usually absent in *C. atrox*, *C. cerastes*, *C. enyo*, *C. exsul*, and *C. lepidus*; and invariably absent in *C. adamanteus*, *C. intermedius*, *C. mitchelli*, *C. pricei*, *C. ruber*, *C. scutulatus*, *C. tigris*, *C. tortugensis*, *C. triseriatus*, *C. v. helleri*, *C. v. oreganus*, and *C. willardi*. Schwenkmeyer reports the rudimentary lung to be a small nonvascular sac, less than 13 mm. long in large snakes, near the apex of the heart. It is so obscure that it is difficult to locate and identify, which may account for some of the species in Schwenkmeyer's list in which the rudiment is occasionally present but usually absent. The *durissus-basiliscus-molossus-horridus* similarity is one reinforced by other characters.

*Respiration.*—Reptiles, with their slower metabolism, are less susceptible than birds and mammals to deviations from a normal oxygen percentage in the air content of their lungs. Boyle (1670, pp. 2013, 2037) found that vipers could withstand a partial vacuum longer than other animals. Tyson (1683, p. 31) doubted whether they breathed at all during hibernation.

A rattlesnake's breathing cycle is quite different from that of man. Man's cycle (when at rest) comprises an inhalation followed immediately by an exhalation and then a relatively long rest. The rest period (apnea) occurs when the lungs are half-full; they are never completely emptied in a normal breathing cycle. The rattler (and presumably all snakes), starting with half-full lungs, first empties them, immediately inhales until they are completely filled, then exhales down to the half-full condition, at which level a long rest period follows. Sometimes several short expiration-inhalation cycles may follow each other rapidly before the long rest.

The rattler's breathing frequency is normally much slower than that of man. As the snake's metabolism increases with higher external (and therefore internal) temperatures, its respiratory frequency correspondingly increases at higher temperatures. Tests of respiration rates obviously must be run on snakes that are not excited; otherwise, defense postures that involve hissing and swelling will affect the results. Schwenkmeyer found the following relationship between temperature and breathing cycles per minute in a red diamond rattler (*C. r. ruber*): 8 cycles at 50° F.; 8 cycles at 60° F.; 4 cycles at 80° F.; 14 cycles at 84° F.; 7 cycles at 90° F.; 16 cycles at 110° F. The erratic fluctuations in the 80–90° range cannot be readily explained; they were probably caused by some condition of the test. However, the doubling of the rate between 50° and 110° F. is probably fairly representative of the effect of the higher temperature, even without increased exertion or muscular activity.

Randall, Stullken, and Hiestand (1944, p. 136) made some interesting tests on the effects of air diluents on the breathing rates of snakes, none of which, however, were rattlers. They found that the effect of carbon dioxide was to decrease the amplitude of the lung ventilation, but to increase the frequency of breathing; excess nitrogen, on the other hand, increased both the amplitude and rate. The oxygen requirement without distress seemed to be between 10 and 15 per cent; a decrease in oxygen content to 15 per cent (that is, below the normal oxygen content of air—21 per cent) seemed to cause no change in respiration (p. 141). An oxygen content of 5 to 10 per cent increased both the frequency and volume of expiration.

It may be observed that the infrequent breathing cycles characteristic of snakes are made possible in part by the posterior air storage reservoir, and in part by the relatively high carbon-dioxide concentration required to initiate another cycle. Furthermore, as a snake's breathing cycle starts by exhausting the lungs, the snake starts its rest period (apnea) with a higher oxygen concentration than does man. With a lower initial carbon-dioxide concentration (because there is a virtually complete removal of the air from the lungs at the start of a new cycle) and a higher terminal carbon-dioxide concentration before a new cycle is initiated, less frequent cycles are normal in snakes, including rattlesnakes, than in man. The effects of gaseous poisons on snakes are discussed under control in chapter 14.

## SQUAMATION

The scales of snakes offer an interesting and important subject for study. To the uninitiated they may appear to comprise a mere haphazard scattering of excrescences on the skin, but this is far from the fact. They are arranged, on both the

head and body, in fairly regular patterns, of which various series can be counted accurately. These series are found to have a considerable consistency within a subspecies, as well as constant differences between subspecies, so that squamation, or scale arrangement, is of the greatest importance in the classification of snakes. Various kinds of snakes that are quite similar in size, form, and color may be readily distinguished by scale differences. Thus, in snake classification and nomenclature, it is essential that the student become familiar with the fundamentals of snake squamation, often referred to by the alternative terms of scalation, scutellation, lepidosis, or pholidosis.

One might think all this detail to be a matter of pseudoscientific affectation, but this is far from the case. Some venomous snakes can be distinguished from non-venomous kinds only by differences in squamation, that is, short of examining their teeth for the presence of fangs. Even among as closely interrelated a group as the rattlesnakes, it is impossible to identify or segregate the several species and subspecies accurately without some knowledge of squamation and of the names that, for convenience, have been assigned to the various scales or to the scutes or plates, as the larger scales are called. It would not be feasible to prepare a key by which the several kinds of rattlesnakes could be distinguished from each other solely by body form, size, pattern, and color; recourse must be had to scale differences, that is, differences in the numbers of scales in certain series, as well as differences in the sizes, shapes, and contacts of individual scales on the head. Furthermore, in badly preserved specimens, the scale numbers and configurations may be ascertained long after the patterns and colors have been lost. It is for these reasons, and not because herpetologists try to make simple things complicated and difficult, that the technicalities of squamation are introduced into snake descriptions and keys.

In a separate chapter on the identification of the different kinds of rattlesnakes (chap. 2), I have set forth certain features of rattlesnake squamation, particularly as related to classification: first, an illustrated glossary explaining the terms applied to the scales of the head and body; second, table 2:7 summarizing the ranges of variation and averages of several important scale series within each subspecies; and, finally, a set of keys to the rattlesnakes, in which various details of squamation become the tools whereby the several species and subspecies may be recognized and distinguished from each other. It is necessary at this point to direct the reader's attention to the illustrated glossary in chapter 2 for an understanding of the terms used in the following discussion of the generalities of rattlesnake squamation, in which trends of variation within the two rattlesnake genera, and some outstanding peculiarities of particular scales in some of the subspecies, are pointed out as examples of variation.

From the sketches accompanying the glossary (figs. 2:83 to 2:91), it will be noted that the scales fall into four broad categories: (1) the head scales; (2) the dorsal series sheathing the body; (3) the enlarged scutes on the belly—the ventral series; and (4) the subcaudals on the underside of the tail.

#### SCALE FORM

As is pointed out in chapter 6 under shedding, the scales of snakes are not separate, removable parts of an outer covering, as they are in most fishes; rather, they are formed by folds or creases in the skin, as a roof might be formed of a single un-

broken sheet of material so folded as to give the impression of separate shingles. This type of formation is advantageous both in allowing flexibility of body movement and in enhancing the strength and durability of the surface. The scales themselves comprise somewhat thickened and hardened sections of the skin, which is thinner and more flexible between them. Yet the actual continuity of the skin surface—of the parts covering the tops of the scales, as well as the folds and creases between them—is shown by the unbroken character of the shed skin when a snake exuviates. In this, every scale top, every fold and crease, is represented in a single flattened sheet, the cast *stratum corneum*. It is by means of this flattening of the creases between scales that the skin is sufficiently enlarged so that, during the shedding process, the narrow neck-section can be slipped backward over the much thicker mid-body part of the snake.

The scales of a snake are of various sizes and shapes, the larger of which are often termed plates or scutes, particularly, the enlarged flat scales on the head. These are separated by creases or sutures, rather than by folds or imbrications such as usually separate the scales.

In many kinds of snakes, both harmless and venomous, the anterior part of the upper surface of the head is covered by a symmetrical arrangement of nine plates. One group of rattlesnakes, those assigned to the genus *Sistrurus*, have these characteristic plates, whereas in the members of the other genus, *Crotalus*, these nine plates, or at least some of them, are broken up into plates or scales of smaller size. These two divergent tendencies—retention of the nine plates intact, or their breakup—are also evident among the pit vipers that have no rattles, thus in part defining the genera *Agkistrodon*, *Bothrops*, *Trimeresurus*, and *Lachesis*.

Posteriorly on the head, and more so on the body, the scales become increasingly imbricate, that is, each scale juts farther over the scale that follows it. The interstices are no longer mere creases but become deep folds, for each scale may overlap its fellow posteriorly by as much as one-fourth of its length. But despite this overlap, the scales are not separate entities, as they appear to be; rather, as can be determined by stretching the skin of a live or freshly killed snake, they are excrescences of the skin produced by thickening and folding.

When a rattlesnake—or, indeed, any snake—is in repose, and not distended with food, one sees only the surface of the dorsal scales, because the thinner skin between them is hidden. But this thin skin is capable of both stretching and flattening, and when a snake moves, or when it is distended by food, the scales will be seen to separate and the intervening areas of thinner skin become visible. This is particularly true of the neck, where the skin between the scales involves a greater part of the total area than elsewhere on the body. When the neck is distended as prey is swallowed, the scales are widely separated from each other, especially transversely. Here the scales are smaller, relative to the thinner skin that surrounds them, than is the case at mid-body or posterior thereto. On the neck when distended, the scales seem but scattered islands in the skin—although arranged in regular rows—whereas elsewhere they more nearly monopolize the area, for the interstices are relatively less extensive. Thus the narrow neck can be distended to permit the swallowing of bulky food, a condition not so necessary toward mid-body, where the body is thickened to provide space for the vital organs, and the food is made slender by the processes of digestion. At the neck, the scales are narrower—

in proportion to their transverse widths—than they are at mid-body, and this relative widening of the scales is further accentuated toward the tail, and along the sides, as well.

Although the dorsal scales are thickened, and, where there is an overlap, involve doubled sections of the epidermis, they do not lack flexibility, although they are less elastic than the skin between.

Many snakes have small longitudinal ridges—the so-called keels—on each dorsal scale, while other kinds have smooth scales. Rattlesnakes belong to the former category; their ridges are particularly evident on the middorsal rows, but gradually weaken on the lateral rows, until the two or three rows nearest the ventrals are smooth (fig. 2:84). The function of the keels is uncertain. Their presence does not affect the lower layers of the skin, which on its interior surface will be found quite smooth. They probably serve as a mechanical reinforcement. Walls (1938, p. 103) has suggested that the keels reduce shininess, thus promoting concealment, which would explain their evolutionary development.

In the Central American rattler (*C. d. durissus*) and its relatives, the normal dorsal keels are further accentuated into protuberances, tuberculations, or bosses that give the snake an exceedingly rough appearance. These are so conspicuous that they were noted as early as 1648 by Marcgravius (p. 240). They are not, however, erectile as was believed by Stedman (1796, p. 195). These tuberculations are most conspicuous on the scale row on either side of the middorsal row, with decreasing intensity laterally. The middorsal row is about as prominently keeled as the fourth lateral row on either side (counting the middorsal row itself as number 1).

Other kinds of rattlesnakes have, in varying degrees, the ridged-row appearance that reaches a maximum in *C. durissus*. The sidewinder (*C. cerastes*) has prominent ridges; in this species the middorsal row is the one most accentuated. Another of our western species with a rough texture is the speckled rattler (*C. mitchelli*). It is considerably more ridged than some of our other southwestern species, such as *viridis*, *ruber*, and *scutulatus*. These differences in keeling and tuberculations are more evident in live than in preserved rattlesnakes.

In addition to the central keel on each dorsal scale, there are divergent striations, directed backward. The lateral edges of the scales are somewhat thickened, with edges blunter than the thin posterior tips. The anterior end of each scale, although covered by the overlap of the scale that precedes it, will be found to have a boundary sharply setting it off from the adjacent skin.

One scale series whose shape has an obvious utility consists of the enlarged transverse plates on the belly, the ventral scutes or gastrosteges, usually termed simply "ventrals." These afford a flat surface on which to crawl; they are smooth and therefore reduce friction as they are dragged over the ground. Also, their sharp posterior edges, acting like tiny ratchets, facilitate the rectilinear type of crawling, and probably the lateral undulatory type as well. The ratchet effect may prevent a snake's backing out when trying to crawl through a wire fence of too small a mesh, as was observed by Campbell (1950, p. 44).

The ventrals are considerably narrower (transversely) at the neck than at mid-body, and again taper at the tail (fig. 2:83). In a typical specimen of the red diamond rattler (*C. r. ruber*), the width—measured across the body—of the ventrals just behind the head was found to be 33 per cent of the width at mid-body; those

just anterior to the vent were 54 per cent of the mid-body width. Measured in the other direction, that is, across each scute, lengthwise of the body of the snake, the dimensions, compared with that at mid-body, were 65 and 59 per cent, respectively. At mid-body the scutes (measured across the body) were 4.6 per cent of the overall length of the snake.

#### SEXUAL DIMORPHISM

Rattlesnakes, like almost all other snakes, exhibit sexual dimorphism in squamation. These differences are particularly accentuated in the number of subcaudal scutes; to a smaller proportional extent in the number of ventral plates; and still less, in fact to an almost inappreciable degree, in the dorsal scale rows. The causes of these dissimilarities are obvious. The males have longer tails than the females because the retracted hemipenes are accommodated in the tail; and, being longer, the tails require more scales to sheathe them. The females, on the other hand, from time to time must carry eggs and young that represent a considerable proportion of the body bulk, and so are favored with additional ventral scutes.

The sexual differences found in rattlesnake scalation, as shown by the statistics of certain homogeneous populations of which adequate numbers were available, have been set forth in detail in two prior publications (Klauber, 1943a, p. 11; 1945, p. 34). It was found that the coefficient of sexual dimorphism<sup>2</sup> in the ventrals—with the females invariably higher—varied from  $\frac{1}{2}$  to 4 per cent, with an average of 2.3 per cent. This indicates a higher count of about four or five ventral scales in the females of most species.

The divergence in subcaudals, with the males always higher, is more conspicuous. The coefficient, as determined separately for each of 21 homogeneous populations of rattlers of 19 different subspecies, was found to vary between 15.5 and 29.3 per cent, with an average of 22.4 per cent. Again this indicates a difference of about five scales; but in this case the percentage is much higher because there are so few subcaudals compared with ventrals.

The results of the investigation of sexual dimorphism in dorsal scale rows (1943a, p. 13; 1945, p. 34) are less consistent. Of the nine cases investigated, the females averaged more scale rows than the males in six series, but only two of these were statistically significant; in the three cases of male superiority, all were statistically significant. But in no case did the coefficient of sexual dimorphism much exceed 1 per cent. The conclusion, therefore, is that sexual difference in the number of dorsal scale rows is not uniform among the rattlers and is of a practically negligible extent. In a few other kinds of snakes the females do have more scale rows to a significant degree. A similar investigation of sexual differences in the labials (1943a, p. 13), although indicating differences above the statistical level of significance, showed them to be neither important nor consistent. In some species the males, and in others the females, were found to have a slightly greater number. In only one group did the difference reach 2 per cent.

In summary, it may be said that sexual dimorphism in squamation among the rattlesnakes is consistent and important only with respect to ventrals and subcaudals.

<sup>2</sup> The coefficient is the difference between the means of the sexes, divided by half the sum of the means, expressed as a percentage. A separate determination is made for each character.

## VARIABILITY

When countable or meristic characters, such as the scales of rattlesnakes, are used in classification—that is, to distinguish subspecies from each other—it is important to know how wide the fluctuations are within a homogeneous population. If we have no knowledge of the intrasubspecific range, or extent of variation, of a certain character, we cannot determine whether a particular specimen that we have newly acquired differs because it really represents another kind of rattler, or because we have happened to secure, purely by chance, one that is higher or lower in some particular scale count than the ones we have studied before. As a measure of variability, a statistic known as the coefficient of variation is widely employed. I have calculated the coefficients of several scale characters in 52 homo-

TABLE 4:5  
VARIABILITY OF SCALE SERIES IN RATTLESNAKES

Character	Coefficients of variation, per cent		
	Minimum	Maximum	Mean
Scale rows . . . . .	1.2	4.7	3.6
Ventrals, males . . . . .	1.1	3.1	2.1
females . . . . .	1.0	3.8	2.1
Subcaudals, males . . . . .	3.7	10.3	6.2
females . . . . .	3.4	11.2	8.1
Supralabials . . . . .	4.3	8.7	6.2
Infralabials . . . . .	4.9	8.5	6.4

geneous groups of rattlers of all the better-known species, involving the scale counts of many thousands of individual snakes. A few of these statistics of variation have been published (Klauber, 1937, p. 36). From this statistical investigation there is evident at once a consistency in consistency; by this I mean that each scale character has a substantially constant degree of variation among all forms of rattlesnakes, but these degrees of variation differ with respect to the several kinds or groups of scales.

A summary of the ranges of the coefficients of variation is given in table 4:5.

It will be observed that the ventrals have the least variation, after which come the scale rows. This is entirely consistent with the usual procedures in herpetology, since these are considered the most important scale characters for classification purposes, which their relative constancy tends to justify. The subcaudals are less important characters in rattlesnake studies than in most other genera because of the foreshortening of the tail by the attachment of the rattles. Furthermore, the counting of the subcaudals is always attended with some uncertainty at both ends of the series; next to the anal plate by the presence of scales not completely crossing the ventrum, which may or may not be considered subcaudals; and posteriorly by the doubtful character of the scales that feather out over the proximal rattle (fig. 2:85). Although, in the rattlesnakes, the subcaudal scales are normally undivided, short runs of divided scales are not unusual. They may occur at any point of the series, and are occasional in all species.

When the range of the coefficient of variation in the several groups of rattlers surveyed was reviewed, it was found that reduced variations are the rule where the territory inhabited is restricted, or is ecologically uniform, as, for example, in the case of island populations.

When, for purposes of differentiating subspecies, countable characters such as scale series are used, it is important to know not only the degree of variability as indicated by the coefficient of variation, but also the nature of the distribution of the individuals about the population mean. An investigation has been made of such distributions (Klauber, 1941, p. 5) and it was found that the ventrals (p. 13), subcaudals (p. 15), and infralabials (p. 17) varied in accordance with what is known as the normal curve of distribution. The supralabial curve was found to be more sharply peaked, that is, with a closer concentration about the mean, than the normal curve.

The question naturally arises whether the degree of variability within homogeneous populations affects the divergence between populations. One might expect that, in the more highly variable characters, the forces of natural selection would have a greater opportunity to produce more rapid and wider changes. Studies were made of six pairs of related populations to see whether the magnitudes of the coefficients of divergence between populations corresponded with the magnitudes of the coefficients of variation within populations, using the five principal scale series—scale rows, ventrals, subcaudals, supralabials, and infralabials—together with the numbers of body blotches and tail rings. The statistics involved have been published elsewhere (Klauber, 1943c, p. 115). It was concluded that in these rattlesnakes the factors or forces that produce territorial modifications are somewhat dependent in their effectiveness on the inherent variability of the characters upon which they operate, for they are more effective on those characters that tend to show a high variability within a territorially homogeneous series. However, the correlation between intra- and intergroup variability was not a particularly close one.

#### ONTOGENETIC VARIATIONS

It is generally assumed in herpetology that scale counts and formations do not change with age—that is, there is no change in any individual snake from birth to death. One might well infer this from the relationship of each shed skin with the skin that succeeds it, for each scale is exactly duplicated in both. However, this is no proof that there may not be a gradual change in the number or form of certain scales as a snake ages. With the idea of investigating this matter, I studied the two largest homogeneous series of the prairie rattlesnake (*C. v. viridis*) available to me, which comprised 833 and 673 snakes, respectively, and reached the conclusion set forth elsewhere (Klauber, 1945, p. 94) to the effect that no changes in scale counts with age are evident. I also determined that there is no evidence of a change in variability with age (p. 95). These conclusions were based on the fact that no significant differences were found between age-groups when each of these homogeneous series was divided into three such groups—juveniles, intermediates, and adults.

It should be emphasized that these conclusions were drawn from series of snakes from which defective young had already been eliminated by natural causes, for the juveniles had already traveled to their winter dens. Should one compare two groups

of snakes, one composed of young immediately after birth and the other of adults, it might seem that a change with age had been demonstrated. This is because any group of embryos, or of young within a few days after birth, is likely to contain a number of defectives whose survival would be of short duration. Such defectives often have quite anomalous scale counts, especially reduced counts accompanying body deformities or adhesions, which distort the averages of their groups from the subspecific normal, and hence might lead one to infer an ontogenetic change in average scale counts when none really exists.

#### DORSAL SCALE-ROW SUPPRESSIONS

Among the most important scale series, from the standpoint of classification, are those that sheathe the dorsal and lateral surfaces of the body—usually known as the dorsal scale rows, or, simply, dorsals. In statistical studies, only the number of rows (counting transversely) at mid-body is usually cited; however, in most snakes, rattlesnakes included, the number of transverse rows varies at different parts of the body to fit the body taper. At any point on the body, there is usually an odd number of scale rows in the dorsal series, comprising a middorsal row plus the same number of rows on each side of the body from this row to the ventrals. The number is usually greatest at the neck, decreasing toward the tail, either by the suppression of single rows, or by the combination of pairs of rows into a single one.

Ruthven (1908), in his studies of the garter snakes, showed that the system of these reductions, particularly the numerical order in which the rows are suppressed, could be used to distinguish species, as well as to indicate relationships between them. Other students, working on other genera, have carried such investigations further, and have found that the point along the body, as determined by the ventral scale opposite which the change occurs, is of importance in taxonomy. Schmidt and Davis (1941, p. 28), Clark and Inger (1942a, p. 163; 1942b, p. 230), and Dowling (1951, p. 131) have devised comprehensive systems of notation whereby such data can be uniformly and completely presented. Breder (1947, p. 321) studied the geometry of symmetry in the scales of fish, and included a short discussion of scale patterns in snakes (p. 406).

In the rattlesnakes scale-row suppressions are more difficult to study than in the slimmer colubrine snakes having fewer rows. In a rattler specimen it is often impossible to determine which of two rows is suppressed, or which two out of three rows are combined to produce a single row. Suppressions may be asymmetrical, so that an even number of rows results, sometimes at mid-body. Points of suppression are more easily located in flattened skins than in snakes preserved "in-the-round." It is often as easy to locate these points by looking for irregularities in the diagonal rows as it is to search for the discontinuance of the longitudinal rows of scales.

In the smaller species of rattlers there is usually a progressive reduction in scale rows from the neck to the anus, whereas in the larger there is often a reduction posteriorly along the neck, followed by an increase which restores or approaches the previous maximum, either at mid-body or slightly anterior thereto. Sometimes a constant number of scale rows may be maintained for one-third or more of the body-length at mid-body. The suppression of scale rows is more regular posteriorly than anteriorly. There is usually much irregularity immediately behind the head, and this is likely to continue rearward for a distance of several head-lengths.

In a tabular summary elsewhere (table 2:7), I have indicated the normal number of scale rows of the several subspecies of rattlesnakes at mid-body, for this is the most important single numerical criterion with respect to the dorsal scale rows. It will be observed that most subspecies fall between 21 and 29 rows, although individuals with as many as 31 occasionally occur in several of the large species, and specimens with as few as 19 may occur in some of the smaller forms.

The number of scale rows one head-length behind the head—a standardized reference point—is usually two or four rows greater than at mid-body, although sometimes equal to the mid-body rows, or even two rows less. Just anterior to the anus the rows usually number four or six below the number at mid-body. Prevalent sequences among various species of rattlesnakes are 29–27–21, 27–25–19, 23–23–17, and 23–21–17; the numbers indicate, successively, the rows one head-length behind the head, at mid-body, and about five scutes anterior to the anal plate.

Returning to the matter of dropping of scale rows, I cite, as examples, the data on two rattlers, the first a Mojave (*C. s. scutulatus*) from central Arizona, the second a red diamond (*C. r. ruber*) from San Diego County:

27 (6 + 7) 25 (5 + 6) 23 (6 + 7) 25 [mid-body] (5 + 6) 23 (5 + 6) 21 (4 + 5) 19.

33 (7 + 8) 31 (7 + 8 R, 6 + 7 L) 29 (5 + 6) 27 (6 + 7) 29 [mid-body] (5 + 6) 27 (7 + 8) 25 (5 + 6 R, 4 + 5 L) 23.

The figures in parentheses indicate the serial numbers—counting upward on the sides, beginning with the lowest lateral row next the ventral scutes—of the two rows that are consolidated into a single row. Where the consolidated rows on the two sides differ, the conditions are indicated separately, with appropriate letters indicating left or right. Row suppression is not only occasionally asymmetrical with respect to the rows suppressed, but is almost always asymmetrical in the longitudinal positions of the suppressions, the consolidation on one side taking place as many as 10 to 20 scales in advance of the corresponding consolidation on the other.

In addition, and this was particularly evident in the *ruber* example, there were short runs of extra scales and of suppressions that I have ignored. These runs in some instances involved only single or pairs of scales, but in other instances entailed as many as six scales longitudinally. At one point, at least, middorsal scales were involved. With such irregularities and asymmetries of dropped rows in a single specimen, I am of the opinion that less of taxonomic value is to be gained from a study of row suppression among the rattlers than is the case in other genera having simpler scale arrangements and a greater uniformity within homogeneous populations. It is for this reason that, in tabulations and keys, I have seldom cited scale rows elsewhere than at mid-body.

The scale rows at the center of the tail are occasionally of some interest, although the intrasubspecific variation is rather high, owing to a considerable irregularity of the longitudinal points of suppression. The generic variation is from 9 to 16.

#### RELATIONSHIP INDICATORS

Scale counts and arrangements are often useful indicators of relationship. For example, the presence of three or more internasals in the various subspecies of the western rattlesnake (*C. viridis*)—as compared with the normal two of all other

rattlesnakes—demonstrated the probable relationships of the subspecies *viridis* and *oreganus* even before intergrades had been found. The same can be said for the divided first infralabials and relatively high ventral scale counts of *C. r. ruber* and *C. r. lucasensis*.

Sometimes these scale peculiarities determine differences between subspecies whose relationship has been confirmed by the discovery of intermediate specimens in the territory between their ranges. An example of such a relationship is that of the southwestern speckled rattler (*C. m. pyrrhus*) and the Panamint rattler (*C. m. stephensi*). These forms differ not only in pattern but in squamation, for each has a peculiarity the other lacks: the first, granules between the rostral and prenasals; the latter, sutured or pitted supraoculars. In this case intermediate specimens having both peculiarities, found in the area between their ranges, rather than scale likenesses, have established the subspecific relationship.

Scale counts are particularly useful in defining trends or clines within subspecies—that is, differences below the level of nomenclatorial recognition. I have illustrated some differences of this nature elsewhere (1937, p. 34; 1943a, p. 15). Sometimes these clines are indicated by gradual modifications in head scales, as is the case in *Crotalus scutulatus*. I have also suggested (1943b, p. 61) a graphical method of combining a number of different countable scale characters to determine whether an intermediate form *X* is nearer another form *A* than it is to a third form *B*.

#### SPECIES PECULIARITIES

Many species of rattlesnakes have certain eccentricities of head scalation quite apart from quantitative differences in the various scale series. These peculiarities seem to be of no adaptive significance, yet they are of value in classification, as I have already shown. They are seldom invariant or completely consistent; usually it will be found that a few individuals of a species will fail to have the distinguishing character; and, correspondingly, the eccentricity will sometimes appear, but with a reduced frequency, in related, or even in unrelated, species.

One of the few scale peculiarities of this type always present in one species is the raised supraoculars—the horns—of the sidewinder (*C. cerastes*). These are invariably evident in sidewinders and never in any other rattlesnake (figs. 2:104 and 2:105). It is true that a beetle-browed effect may be noted in some other species—the Lower California rattler (*C. e. enyo*), for example—but, when comparisons are made, it will be observed that the raised supraocular is not nearly so distinctive as the exaggerated horn of the sidewinder. What the purpose of the horn may be is not known. I once suggested that it might serve to leave the eyes exposed, yet protected from the drift, as the snake lies partly buried in the sand; but now I doubt that the snake buries itself often enough to just the required depth to derive such a benefit from the horns. The theories that the horn comprises either a shade for the eye or a radiator of heat are doubtful in view of the sidewinder's nocturnality.

Ornamental appendages of this type are more extensive and bizarre in some snake genera than in rattlesnakes—the snout protrusions of the Madagascan snakes of the genus *Langaha* and the horns of the rhinoceros viper (*Bitis nasicornis*), for examples. The dubious suggestion has been made that these fantastic ornaments

in such species as the horned viper of the Sahara (*Aspis cerastes*) might attract insects or birds, when the creatures lie almost buried in the sand (Griffith and Pidgeon, 1831, p. 369, repeating statements by Pliny, 1855-57, vol. 2, p. 285; book viii, chap. 35, and by Solinus). Pliny made an alternate suggestion that they might serve as feelers (vol. 3, p. 45; book xi, chap. 45). Cowles (1953, p. 14) says the horns of the sidewinder may be just a whim of evolution. Of the two Saharan vipers, occupying somewhat the same faunal niche in that desert that our sidewinder does in the American Southwest, one, the sand viper (*Aspis vipera*), is without horns, while the other, the horned viper (*Aspis cerastes*), has longer but slenderer horns than the sidewinder. There is a similar pair with and without horns in the genus *Bothrops*. There seems no logical explanation for this difference in two creatures so closely related, and of such similar habitat and habits.

Another peculiar group of scales always present in one species of rattler, but in no other, is the sharply bent internasals and partly bent canthals that give the ridge-nosed rattlesnake (*C. willardi*) its name (fig. 2:108). One might assume this snout peculiarity to be a digging device, yet this rattler inhabits rocky situations. A feature largely restricted to the widespread western rattlesnake (*C. viridis*) is the presence of more than the two internasals normal to other rattlers. Eighty-six per cent of the northern Pacific rattlers (*C. v. oreganus*) have three or more internasals; and, of the other subspecies of *C. viridis*, 90 per cent or more have this unusual arrangement (fig. 2:116). Rare, indeed, is the rattlesnake of any other species that has it, even as a chance anomaly.

It is characteristic of the subspecies of the speckled rattlesnakes, *C. m. mitchelli*, *C. m. pyrrhus*, and *C. m. muertensis*, but not of *C. m. stephensi*, that the rostral is separated from the prenasals by rows of small scales or granules (fig. 2:113). This peculiarity is occasional—to the extent of about 17 per cent—in the Arizona black rattlesnake (*C. v. cerberus*), but is quite rare in other species. The Panamint rattler (*C. m. stephensi*), although lacking these extra scales so characteristic of the other *mitchelli* subspecies, has its own irregularity, namely, conspicuous sutures or pits in the supraoculars (fig. 2:124). This character is occasionally observed in the related *muertensis*, but rarely in any other kind of rattler.

The red, San Lucan, and Cedros Island diamondbacks (*C. r. ruber*, *C. r. lucasensis*, and *C. exsul*) are characterized by a high proportion with divided first infra-labial scales, to the extent of 91, 87, and 99 per cent, respectively (fig. 2:132). These scales are rarely present in other species, except in the *durissus* subspecies *tzabcan*, and, to a lesser degree, in *culminatus* and *terrificus*. *C. exsul* is further notable for the prevalence of intergenials (fig. 2:145).

The subspecies of the rock rattlesnake (*C. lepidus*) are notable for usually having a vertically divided upper preocular, the anterior half of which is higher than the posterior and curves over the canthus in front of the supraocular (fig. 2:114). A similar split is often noted in the speckled rattler, especially the subspecies *C. m. pyrrhus* from certain areas, but in this snake the forward part is not so high, nor does it curve over the top of the head, as it does in the subspecies of *lepidus*. Another peculiarity, not so conspicuous or consistent as the others, but useful in identification, is found in the Mexican lance-headed rattler (*C. polystictus*); this comprises a pair of narrow intercanthals, usually about twice as long as wide (fig. 2:134).

Some species of rattlesnakes are characterized by unusual contacts between certain scales. For example, in the subspecies of the small-headed rattlesnake (*C. intermedius*) the loreal almost always touches a supralabial, and frequently the upper preocular as well (fig. 2:118), a condition found in no other species. A peculiarity of *pricei* is a broad contact between the first supralabial and the postnasal (fig. 2:112). These scales are separated in most species, and touch only narrowly in the others.

I have called attention to only a few of the many differences in scale shapes, numbers, divisions, arrangements, and contacts that characterize rattlesnake subspecies with varying degrees of consistency. Without the recognition and use of these characters in keys, it would usually be impossible to classify individual snakes with accuracy.

#### SCALE HOMOLOGIES AND DERIVATIONS

As has been stated, the sizes and arrangements of the head scales are useful in indicating, not only species differences, but likewise species relationships. The rattlesnakes of the genus *Crotalus*, possessed, as they are, of many subdivisions of the head scales as compared with the more primitive and standardized nine-scale crown retained by the rattlers of the genus *Sistrurus*, exhibit certain directional trends—different in the several species and species groups—in the manner and extent in which the primitive scales have been broken up. Certain scales are much more subject to change than others. These changes vary in degree, from some species that retain many resemblances to *Sistrurus*, as does *C. pusillus*, to the other extreme in *C. mitchelli* and its subspecies, in which the scales have reached the ultimate in subdivision. In the latter species, more than in any other, it is often impossible to determine, by their present forms and locations, the original scales from which the present fragments and granules were evolved.

Of the head-scale groups, the labials are the least subject to modification; although varying in number, and to some extent in relative size, they are substantially of similar form—rows of scales edging the mouth above and below—in all of the rattlers. Abnormalities are occasional in nearly all subspecies, but consistent differences are sufficiently rare to be worthy of comment: these are the transversely divided first infralabials of *ruber* and its relatives (fig. 2:132), carried farther into the intergenials of *exsul* (fig. 2:145); the elongated last supralabials of *C. m. mitchelli* (fig. 2:148); and the blunt first infralabials of *C. stepheneri*.

Of the single or paired head scales, the most constant are the rostral, the nasals, and the supraoculars. It is especially notable that, although the other seven crown plates of *Sistrurus* are, in *Crotalus*, broken up in varying degrees, the supraoculars remain, changed only in relative size, except for the pinnacles of *C. cerastes* (figs. 2:104 and 2:105) and the irregular sutures and depressions found in *C. m. stephensi* (fig. 2:124).

The other scales of the crown—the internasals, prefrontals, frontal, and parietals—all break up in varying degrees in the species of *Crotalus*, but more so in the northern than in the southern forms.

The internasals are retained virtually intact in *durissus*, *basiliscus*, *molossus*, and their allied forms, as well as in *lepidus*, *triseriatus*, *pusillus*, and related small species of the Mexican plateau. They decrease in size in the northern forms such

as *adamanteus*, *atrox*, and *horridus*; and, in *viridis*, are subdivided so that there are usually four instead of two (fig. 2:116).

The prefrontals are also retained intact in *durissus*, *basiliscus*, and *pusillus*, and less frequently in *molossus*, although occasional individuals are found in which these scales are irregularly sutured. In most other species, they are subdivided into two series: one to three moderately large outer scales—the canthals—and a group of intercanthals between. With an increased subdivision of the intercanthals, these scales have a tendency to become ridged and tuberculate, instead of remaining flat as in *durissus* and *pusillus*, in which their primitive forms and sizes are retained. Some of the smaller rattlers, such as *lepidus*, *pricei*, and *triseriatus*, as well as *scutulatus* among the larger, generally have from one to four flat intercanthals; thus they are intermediate between *durissus* and such forms as *atrox*, *ruber*, *viridis*, and *horridus*, in which there are many small and quite irregular scales in the intercanthal area. *C. enyo* and *tigris* are characterized by ridged and knobby intercanthals; *polystictus* by an elongated pair of flat scales. The canthals themselves tend to increase from one on each side in the smaller species to two or three in the larger.

No species of *Crotalus* retains the single frontal of *Sistrurus*, although rarely an aberrant individual may have a single scale that occupies the anterior part of the intersupraocular area. But it is usually characteristic of those species of *Crotalus* that retain the internasals and prefrontals intact to have a pair of enlarged flat scales bridging the anterior section of the intersupraocular gap, followed posteriorly by smaller scales of more irregular size and disposition. Paired anterior intersupraoculars are characteristic of *durissus*, *basiliscus*, *molossus*, and *scutulatus*. The maximum subdivision of these scales is reached in *ruber*.

Paired and contiguous parietals of the colubrine type that characterize *Sistrurus*<sup>a</sup> are never found in *Crotalus*. In the latter genus, the most recognizable parietal remnants are to be noted in *scutulatus*, in the form of a flat crescentic scale at the inner, posterior border of each supraocular (fig. 2:130). Scales of this form are also noted in *durissus* and *molossus*, unfortunately with sufficient frequency to inhibit their use as invariable diagnostic characters for *scutulatus*. The latter species is also peculiar in having the entire parietal area occupied by flattened scales of somewhat enlarged size, as compared with the smaller ridged scales on the posterior half of the head. Thus there is apparent a ghostly outline of the former parietals.

Scale homologies are moderately consistent on the sides of the head, although somewhat disturbed by the indentation of the pit. In any case, there is here no basic difference between *Sistrurus* and *Crotalus*, such as characterizes the scales on the crown. The prenasals are usually intact except in *mitchelli*, in which species (with the exception of *C. m. stephensi*) they are subdivided anteriorly to interpose a row of granules adjacent to the rostral (fig. 2:113). In this species, if this subdivision of the prenasals is not complete, the anterior edges are usually frayed or sutured, often producing partial separation by means of a small scale on each side next the internasals or above the supralabials. In most rattlesnakes the prenasal is larger than the postnasal, with an increased proportion of the latter scale occupied by the nostril itself in the larger species. The prenasal curves over the top of the postnasal in such species as *pricei* and *intermedius*, and under the postnasal in

<sup>a</sup> Often split transversely in the species *S. ravus*.

*lepidus*. In *polystictus*, either a canthal, an internasal, or an extra scale virtually becomes a supranasal, by separating the regular nasals just above the nostril; and in *pricei* the first supralabial virtually does the same below (fig. 2:112). In *cerastes* the nasals are usually conjoined above the nostril, a condition also prevalent in *lepidus*.

The loreal is variable both in its size and in its contacts with adjacent scales. It is usually triangular in form and slightly higher than wide, although the reverse is often true in *lepidus*. An upper loreal, split off from a canthal, is sometimes present; and it is characteristic of *durissus*, *basiliscus*, *molossus*, and their relatives that a row of small scales (an upper loreal and several postsupraloreals behind) are usually interposed just below the canthus, either partly or entirely separating the upper preocular from the canthal, which, in those species, is a full-fledged prefrontal.

Below the loreal—except in the forms related to *intermedius*, in which the loreal is in contact with one or more supralabials—lies the pit and, anterior to the latter, a series of small scales that have been termed prefoveals. They lie in the triangular area bounded by the pit border or lacunals, the loreal, postnasal, and supralabials. They vary greatly in number and arrangement; they are usually more numerous in the larger species, as if their number depended on the area to be covered. In some forms, notably *molossus*, *basiliscus*, *exsul*, and *cerberus*, the prefoveals are usually carried forward to the rostral, thus preventing the normal contact between the prenasal and the first supralabial (fig. 2:121). Where this contact is not completely interrupted in these forms, there is often a single extra scale, a postrostral, at the rostral-prenasal-supralabial junction point.

The preocular scales, an upper and a lower, are fairly consistent among the rattlesnakes. The upper is much the larger of the two; it is usually entire, but is quite consistently divided vertically in *lepidus*, and is irregularly broken up in *mitchelli*. It is in contact with the postnasal in some species, whereas in others this contact is prevented by the junction of the loreal and a canthal, or by upper and lower loreals. In some forms, notably *triseriatus*, the upper preocular is tilted upward anteriorly, curving over the canthus, and in this species it is sometimes divided as in *lepidus*.

The lower preocular, a thin crescentic scale, forms the upper border of the pit in most species, and is in contact with the loreal beyond. In the forms allied to *intermedius*, it usually enters the pit, and thus its normal contact with the loreal is prevented (fig. 2:138). Occasionally the lower preocular is divided by a vertical suture; and in *C. m. mitchelli* an extra scale often appears between the preoculars, near their midpoints (fig. 2:148). Below the lower preocular there is sometimes a diagonal scale (called by Gloyd the lacrimal) of somewhat uncertain status. It is with difficulty distinguished from the suboculars, and, because of the peculiar conformation of the skin at this point, one is often not sure whether or not it should be considered a member of the orbital series.

No sharp distinction can be made between sub- and postoculars, and the scale arrangements between suboculars and labials are so irregular that one cannot with certainty designate the "number of scale rows between the labials and orbit" unless a single reference point be specified, as, for example, immediately below the pupil. However, it is usually possible to determine definitely which, if any, suboculars are in contact with the labials, as well as the serial numbers of the labials so in

contact, and these data will be found of use in classifications. Subocular-supralabial contacts are normal in *Sistrurus*, *polystictus*, *pusillus*, *pricei*, and the *intermedius* groups; they are frequent, but not invariable in *lepidus* and *triseriatus*; occasional in *tigris*; and are quite rare in the other forms. The anterior subocular is the scale that most frequently makes this contact; in *intermedius* both anterior and posterior suboculars usually touch the labials (fig. 2:138), and this is sometimes, but less often, the case in *pricei*. Sometimes the numbers of the supralabials touched by the anterior subocular give a species clue; for example, the third and fourth are contacted in *S. miliarius* (fig. 2:99), and the fourth and fifth in *S. catenatus* (fig. 2:98). The postoculars are smaller and more irregular than the pre- or suboculars. Temporals of the colubrine type are absent in both *Sistrurus* and *Crotalus*.

On the underside of the head there are only a few consistent deviations, of any diagnostic value, from the normal generic pattern of scale characters. Mention has already been made of the division of the first infralabials, almost invariable in *ruber*, *lucasensis*, and *exsul*, and frequent in *tzabcan* and *mitchelli*. The posterior point of the mental is sometimes cut off to form a submental (fig. 2:146); and intergenials, formed by cutting off the posterior tips of the first infralabials, are sometimes present, particularly in *exsul* and *ruber* (fig. 2:145). The most distinctive modification in this part of the head is to be found in *stejnegeri*, in which the normally pointed posterior ends of the first infralabials are blunt and, instead of being interposed between the genials, terminate against them. In *molossus* and *scutulatus* the genials are sometimes split transversely.

#### SCALE CHARACTERS AND CLIMATE

In 1941 (p. 73) I published a study indicating that, in species of snakes occupying both the coastal and desert areas of San Diego County, the desert specimens—in most subspecies—tended to have more ventral plates on the average than those from along the coast. Wade Fox (1948, p. 252) performed some exceedingly interesting and important experiments showing the effect of prenatal temperature conditions on scale counts of the young. He procured gravid female garter snakes from a limited locality, and, having divided them into two groups, he submitted one group to a higher temperature than the other during the period of the embryonic development of their young. The young born to the mothers in the cooler room had significantly fewer scale rows, supralabials, ventrals, subcaudals, and postoculars than those whose mothers had been kept warmer during gestation. Fox (p. 261) is careful to emphasize that this experiment does not prove that the geographic variation of scale characters is without a genetical basis.

There is little doubt that temperature—and possibly humidity as well—does affect the scale counts of rattlers, especially their scale rows and ventrals. However, as will be mentioned in discussing correlation, body size is also important; the larger snakes—speaking in terms of population averages, not individuals—have more scales. Where these two effects are additive, that is, where the larger form also occupies a warmer area, the differences are usually marked; but where the two effects work at cross-purposes, the correlation is usually less consistent.

## CORRELATIONS

Among the snakes there are two kinds of scale correlations (that is, concomitant variations in two groups of scales) of sufficient practical interest to deserve comment. The first kind entails correlations within homogeneous populations and would supply answers to such questions as, whether, in such populations, individuals with more than average ventrals also have higher than average subcaudals; whether a particular snake with a high number of labials on the right side of the head is likely to exceed the average on the left side; and whether one may properly infer the presence of above-normal infralabials from the presence of above-normal supralabials. The second kind of correlation would answer the same questions, but would consider subspecies as the units of comparison in a generic complex, rather than individual snakes. Size may also be brought in as a criterion, the question being whether the larger species tend to have more scales in the various series than the smaller.

With regard to the first type of correlation—that involving individuals within a homogeneous population—I investigated it and evolved the following conclusions applicable to rattlesnakes; the pages cited all refer to Klauber, 1945:

Bilateral correlation is evident in scale peculiarities or particular contacts; any condition existing on one side of the head is much more likely to be duplicated on the other than if its occurrence there were based purely on chance (p. 13). A high bilateral correlation is also evident with respect to the numbers of particular groups of scales on the two sides of the body (p. 21). Special studies were made of the labials, including horizontal correlation (the relation of the supralabials on the right with those on the left), vertical (the relation of the right supralabials with the right infralabials, and the same relation on the left), and diagonal correlation (the right supralabials with the left infralabials and vice versa) (pp. 23–28). It was found that the horizontal correlations were significantly higher than the vertical or diagonal, which latter two did not differ significantly from each other. All correlations were found to be positive and significant, but the vertical and diagonal were of a relatively unimportant magnitude compared with the horizontal. Briefly, in somewhat simpler terms, this means that if a rattler has a higher than average number of supralabials on the right side of the head, there is a strong likelihood that there will be a high number on the left; but the likelihood of higher than normal infralabials, on either the right or left, is much reduced.

No correlation between dorsal scale rows and ventrals was disclosed (p. 35), nor was any apparent between scale rows and subcaudals (p. 36). A slight correlation was found between ventral and subcaudal scales, more in the males than in the females. A moderate correlation was evident between various pairs of head scales, but by no means in all of the pairs tested (p. 38). There was some correlation between scale rows and labials, but none was found between ventrals and labials (p. 40).

In a homogeneous population, individual rattlers that have proportionately longer tails than the group mean also have more subcaudal scales than the group mean (p. 81). Large male rattlesnakes in such a population tend to have more ventral scales than the average of the population, but the same was not found to be true of the females (p. 88). Altogether, it may be said that scale-count correlations

of this type—correlation in a single individual, in its deviations from group averages—is the rule rather than the exception.

The other type of correlation is that in which all the available specimens of a species or subspecies are combined into a unit (by use of their averages) in a study of intrageneric variation, to see whether there are concomitant fluctuations in the scale counts running through the subspecies so as to comprise a generic pattern.

These studies indicate that certain scales can at once be eliminated from consideration, thus simplifying a survey of the rest. No generic correlation is found to exist between the subcaudals and the other scales. On the contrary, as might be expected, the number of subcaudals depends on the relative length of the tail—the conspicuously long-tailed species tend to have high numbers of subcaudals. This tail proportionality (Klauber, 1943a, table 19), which strongly affects the number of subcaudals, has no particular relation to body size, for the long-tailed rattlers include some of the largest (e.g., *durissus*) as well as the smallest (*miliarius*, *stejnegeri*) of rattlesnakes.

As to the various scales on the crown of the head—the internasals, canthals, intersupraoculars, and the total scales in the prefrontal area—these also are found to have little relation to other series of scales, or to the size of the species. The members of the genus *Sistrurus*, except for an occasional aberrant, especially in *ravus*, have a uniform pattern of nine plates on the crown; and even in the genus *Crotalus*, the trends in these head scales seem to follow certain lines of descent, instead of being correlated with other scales. Nor is there any indication that size is important in determining the extent of the subdivision of the scales on the crown. For example, there are large rattlesnakes with many scales on the crown (e.g., *adamanteus*) and other large ones with few (*durissus*); and the same independent variation may be observed in some conspicuously small species, *willardi* being an example of a form having many scales on the crown, whereas another small species, *pusillus*, has but few.

Upon the omission of these scales from consideration, we are left with the dorsal scale rows, ventrals, and labials, whose generic correlations we shall now review. There is, first, an unquestioned correlation between the supra- and infralabials—rattlesnake species or subspecies that have high numbers of scales lining the upper edge of the mouth, generally have high numbers below as well. The supralabials in rattler subspecies—citing the averages for each subspecies—vary from as few as 9.0 in *pricei* and 9.1 in *omiltemanus*, to as high as 17.4 in *molossus*; the corresponding range of the infralabials is from 8.9 in *omiltemanus* and 9.1 in *intermedius* to 17.7 in *ruber* and *lucasensis*. Usually, the difference between the supra- and infralabials averages less than one scale, with the infralabials almost invariably the higher. The snake with the greatest difference is the eastern diamondback (*adamanteus*), in which the upper labials average 14.2 and the lower 17.4, a difference of 3.2. A few subspecies have more upper than lower labials; of these *lepidus*, with an average difference of nearly one scale, is outstanding.

In view of the undoubtedly close correlation between the upper and lower labials, I shall hereafter combine the labials into a single unit, in ascertaining their correlations with the other scale series.

The three series of scales—dorsal scale rows, ventrals, and labials—may be taken in pairs and their correlations assessed, the question being: is there a concomitant

variation of one series with another; for example, do the rattler species with the higher number of scale rows tend to have more ventrals and labials? The answer is yes with every pair, not an exact correlation by any means, but an undoubted trend from which certain species stand out as conspicuous exceptions.

The closest correlation is that between ventral scales and labials, the relationship being expressed approximately by the equation  $B = 0.11V - 4$ , where  $B$  is the average number of the labials on one edge of the jaw (the total labials divided by 4) and  $V$  is the average number of ventrals in the males. I do not mean to suggest that there is exact adherence to this regression line; but the correlation is sufficiently close so that nearly all subspecies will fall within one and a half labial scales on either side of the line. The principal deviators are *totonacus*, *lepidus*, *klauberi*, *intermedius*, *omiltemanus*, and *pricei*, which have fewer labials than anticipated from the equation, the last three conspicuously so; and *meridionalis*, which has slightly more.

The correlation between scale rows and ventrals is less consistent, although quite evident. The relationship is expressed by the equation  $R = 0.13V + 3.4$ , although many species and subspecies deviate considerably from this average generic line. The subspecies with more than two scale rows above the regression line are *durissus*, *culminatus*, *terrificus*, *unicolor*, *adamanteus*, *meridionalis*, *willardi*, and *catenatus*. Those falling more than two rows below are *omiltemanus*, *intermedius*, *pricei*, *stephensi*, *muertensis*, and *totonacus*.

Finally, there is an unquestioned correlation between scale rows and labials; snakes with high numbers of scale rows tend to have high numbers of labials. Roughly speaking, the relationship of the two is represented by the equation  $B = 1.16R - 15$ , where  $B$  is the average number of labials along one edge of the mouth, and  $R$  the number of dorsal scale rows at mid-body. For example, snakes with 23 scale rows have about 11.7 labials, whereas those with 27 rows average about 16.3. A considerable number of subspecies differ by more than one and a half labials from the expected number, and a few by as many as two labials. These are *pyrrhus*, *muertensis*, *nuntius*, *horridus*, and *cerastes*, which have more labials than would be expected under this formula; and *durissus*, *culminatus*, *terrificus*, *unicolor*, *adamanteus*, and *meridionalis*, which have fewer.

The question naturally arises as to whether these correlations between series of scales may not be produced by some more fundamental condition that affects all alike. On the assumption that there are mechanical interrelations between skin thickness, scale size, and body size, one should naturally expect higher numbers of scales in the larger species compared with the smaller, although by no means proportional to the increase in body size. Such a correlation is found to exist. In determining the correlations, the criterion of length for each subspecies has been taken as that of a large male, as given in table 4:1. These lengths, in turn, have been plotted against the average scale counts, thus securing a scatter diagram in which each subspecies is represented by a single point.

A moderate degree of correlation is found between size and the number of dorsal scale rows, the smaller kinds of rattlers usually having fewer rows. The most conspicuous deviators are the three subspecies of *willardi*, and *stejnegeri*, *exsul*, *polystictus*, and *caliginis*, which have more rows than might be anticipated from their sizes; and *atrox*, *totonacus*, *horridus*, and *atricaudatus*, which have fewer.

There is a quite evident correlation between ventral scales and size, although the adherence of the several subspecies to the regression line is by no means close, for there is much scattering. Those that deviate most are *stejnegeri*, *exsul*, *intermedius*, and *omiltemanus*; and the stunted races *muertensis*, *nuntius*, *caliginis*, and *decolor*, all of which have higher ventral scale counts than might be anticipated from their sizes. Departing in the other direction—that is, having fewer ventrals than are to be expected—are *adamanteus*, *atricaudatus*, *durissus*, *culminatus*, *terrificus*, and *catenatus*. It is as though these subspecies, living in areas more favorable to bodily growth than their progenitors, have not yet had time to increase their ventral scales

TABLE 4:6  
TRENDS OF SQUAMATION WITH LENGTH

Length over-all of a representative large male (mm.)	Ventrals	Scale rows	Labials (one side of one jaw)
500	138	20.9	10.5
600	149	22.9	11.9
700	157	24.3	13.0
800	164	25.1	13.9
900	170	25.6	14.7
1,000	174	26.0	15.2
1,100	176	26.4	15.6
1,200	178	26.6	15.8
1,300	179	26.8	16.0
1,400	180	27.0	16.1
1,500	181	27.2	16.1
1,600	182	27.4	16.2

in proportion to their changes in size. Also, it may be noted that these species and subspecies occur in more humid areas than most other rattlesnakes. The effect of temperature and possibly of humidity on scale counts has already been mentioned.

Correlation is also evident between body size and labials, although slightly more evident between head size and labials, as might well be anticipated. Forms with conspicuously more labials than would be expected (from the generic trend line) are *stejnegeri*, *muertensis*, *exsul*, and *molossus*; on the other hand, *totonacus* is low.

Table 4:6 shows the approximate courses of the three trend lines that have been developed.

These three lines are parabolic in form; the increase in number of scales, per unit increase in length, is much higher in passing from small to medium-sized species than in going from the latter to large species. The incremental percentages in scale counts for a 60 per cent increase in body size are as follows:

Body-length increases of 60 per cent	Percentage increases in scale counts		
	Ventrals	Scale rows	Labials
From 500 to 800 mm.	19	20	32
From 1,000 to 1,600 mm.	5	5	7

Thus it appears that a 60 per cent increase in the size of small rattlers produces a much greater increase in the numbers of scales in these series than a corresponding percentage increase from medium- to large-sized species. It should be reiterated that these generic trend lines are only approximate, for the deviations of individual subspecies from the lines are quite extensive.

The subspecies that deviate most from the trend lines illustrate one factor, namely, the resistance to change in the number of scales in a series, after size has been modified by the effects of ecological conditions. A stunted race is likely to retain, in some degree at least, the scale counts of its ancestors, so that it usually has more scales than the truly small species of corresponding size. Thus we note, in such stunted races as *muertensis*, *nuntius*, and *caliginis*, some reductions in scale counts, compared with the races *pyrrhus*, *viridis*, and *helleri* from which they were derived, but the process has not been carried as far as may some day be evident. This is also true of the relationship between *exsul* and *ruber*. It is clear that squamation is more stable than size.

These trends of correlation of size with scale counts are occasionally reversed. An example of such a condition is to be found in the western diamond and red diamond rattlers (*C. atrox* and *C. r. ruber*). The latter is clearly derived from the former, as shown by resemblances in form and pattern; but although *ruber* is a smaller snake than *atrox*, it has, on the average, more scale rows, ventrals, and labials, than its larger relative, and this despite the fact that it lives in a cooler area.

Although the correlation of scale counts with size is moderately consistent when species are used as the units of comparison, it is not always consistent with respect to adjacent populations within a subspecies, or between adjacent subspecies. Here the effect, already mentioned, of increased temperatures in producing higher scale counts, may have counterbalancing results. Where the two effects tend to have the same direction, that is, where the smaller species occupies the cooler area, then the correlation is likely to be quite consistent; but where the contrary is true, the results are unpredictable. The Mojave Desert sidewinder (*C. c. cerastes*) is smaller and occupies a higher, cooler area than the Colorado Desert sidewinder (*C. c. laterorepens*), and all of the scale counts of the latter average higher than the former. The same is true of the southern Pacific rattler (*C. v. helleri*) when compared with the smaller Coronado Island rattler (*C. v. caliginis*). But although the prairie rattlers of northeastern Colorado are smaller than those of central South Dakota, they occupy a warmer area and are higher in some scale counts and lower in others (Klauber, 1937, p. 34). Similarly, the western diamond rattlers of south-central Arizona, although somewhat smaller than those of central Texas, have more scale rows and ventrals. The area they inhabit is drier and somewhat warmer. These and other examples make it clear that temperature effects, when in opposition to size, may upset the effects of size differences. But where the temperature differential—and possibly that of humidity, also—is moderate, or the size difference between the populations is great, then the correlated differences in the scale counts, especially the dorsal scale rows and the ventrals, are likely to be considerable, and entirely consistent with size trends.

## COLOR AND PATTERN

"As touching Serpents, wee see it ordinarie that for the most part they are of the colour of the earth wherein they lie hidden: and an infinite number of sorts there be of them." So said Pliny many centuries ago (translation by Philemon Holland, 1601, vol. 1, p. 208).

Rattlesnakes are indeed of many colors and patterns. Although their colors can often be attributed to procrypsis or concealing coloration, this is by no means invariably the case. In general, rattlesnakes are blotched, as is usually true of heavy-bodied, slow-moving snakes (Klauber, 1931b, p. 45). If any pattern can be considered typical of the rattlers, it comprises a primary series of dark dorsal hexagons, each of which is bordered by a row of light scales. The interblotch color is usually intermediate in shade between the blotches and their light borders. Laterally, there are from one to three rows of smaller auxiliary blotches, alternating with the dorsal series and with each other. Posteriorly, the dorsal blotches merge with the laterals to form crossbands, a characteristic of many species. The body marks are less sharply defined posteriorly than toward the head. There is a great difference between species of rattlers, and indeed within species, with respect to the definiteness with which the dorsal blotches are outlined and limited. In some, the blotch borders are sharply edged, whereas others have blotches that are hardly more than ill-defined concentrations of stippling. In most species, the patterns become less clear when the snakes become adult. The ventrum is usually mottled with irregular dark marks on a lighter background.

The dorsal blotches, although most often hexagons, vary in the several species through a diversity of shapes, such as diamonds, rectangles, and ellipses. While the anterior blotches are usually closed on the sides, this is not invariable. In the Arizona ridge-nosed rattler (*C. w. willardi*), the lateral blotch-edges fade imperceptibly into the ground color (fig. 2:72); and in the northern blacktail (*C. m. molossus*), even the anterior blotches usually continue down the sides as narrow, dark streaks (fig. 2:107). Some rattlers, including the subspecies of *C. horridus* (figs. 2:30 and 2:31) and *C. lepidus* (figs. 2:35 and 2:36), are cross-banded rather than blotched, although the bands are rather irregular. In one form, the Arizona twin-spotted rattler (*C. p. pricei*), the major dorsal blotches are divided into two series, on opposite sides of the middorsal line (fig. 2:46); and in another (*C. polystictus*) there are rows (sometimes separated middorsally) of ellipses with their major axes lengthwise of the snake (fig. 2:136).

While, as pointed out elsewhere (p. 237), freak rattlers with longitudinal stripes are occasionally found, such marks are not normal, except in the subspecies of the Neotropical rattler (*C. durissus*) and in *C. unicolor* (figs. 2:19 and 2:60). The snakes of this group have a pair of dark stripes on the neck, separated by a lighter middorsal streak. These marks extend from one to four head-lengths behind the head, posterior to which they are replaced by diamonds.

Rattlesnake heads are usually marked with a dark streak passing backward and downward through the eye toward the angle of the mouth; this streak is set off by light borders or a light background. The top of the head, especially the supraocular scales, generally contains various light marks, although in many species these dis-

appear with age. Rattlesnake tails are characteristically barred with dark cross-bands or rings on a lighter background. Sometimes the tail colors are sharply differentiated from those of the body, a characteristic, for example, of the diamond-backs allied to the western diamond (*C. atrox*), which have alternate light-gray and black rings on the tail, whereas the body color is tan, red, or gray (fig. 2:125). In *molossus* the tail is usually solid black, quite dissimilar to the rest of the body, which is olive-green or olive-brown. A tendency toward longitudinal striping on the tail is to be noted in a few rattlers, particularly the ridge-nose (*C. willardi*) and the Cedros Island diamondback (*C. exsul*). The reason for these color contrasts between the body and tail is not apparent, unless it be to attract visual attention to the place from which the sound of the rattle is emanating. When a snake rattles, the tail is somewhat blurred by the rapidity of the vibration, but as the motion is transverse, rings are less blurred than stripes would be.

#### COLOR AND ITS APPLICATION

A close examination reveals that the rattlesnake's color is usually applied in the form of dots, stippling, or punctations. Sometimes the separate dots are clearly evident, as, for example, in the western diamond (*C. atrox*), the southwestern speckled rattler (*C. m. pyrrhus*), and the tiger rattlesnake (*C. tigris*); in others the dots can be distinguished only upon magnification. Rahn (1941, p. 228; 1942a, p. 178), in discussing color changes in the prairie rattler (*C. v. viridis*), has shown how intermediate colors result from the interactions between melanophores and guanophores. It is probable that rattlesnake colors are produced by the relative concentrations, superpositions, and arrangements of four types of pigment cells: melanophores (black), guanophores (white or yellow reflecting), lipophores (yellow to orange-red), and allophores (red to violet). Melanic granules in the intercellular spaces are also important.

Rattlesnake blotches, marks, and ground colors vary from white to black, through many hues, shades, and tints. White, or almost white, is not at all uncommon ventrally, and many species have rows or clumps of white scales dorsally or laterally. Probably the rattler most nearly deserving the name "white rattlesnake"—exclusive of albinistic freaks—is a color phase of the southwestern speckled rattler (*C. m. pyrrhus*) that occurs in the Tinajas Altas Mountains of southern Yuma County, Arizona (Klauber, 1936a, plate 20), although even this snake has patches of dark scales on the back.

Jet-black rattlers are to be found as an adult color phase of several subspecies, including the eastern massasauga (*S. c. catenatus*), the Mexican pigmy rattler (*S. ravus*), and the timber rattler (*C. h. horridus*). In some areas, the Arizona black rattler (*C. v. cerberus*) is almost entirely black (fig. 2:65).

Although most rattlesnakes run to grays and browns—soft colors popular for decorative schemes during the mauve decade—bright colors are by no means absent from their patterns, but such colors are less conspicuous than in unicolored snakes. Certainly Ruskin's dictum (1875, p. 191), that rattlers are never brightly colored, is far from accurate. Several kinds of rattlesnakes include bright yellow in their patterns, the timber rattlesnake (*C. h. horridus*), and the northern blacktail (*C. m. molossus*) from some mountain areas, being examples. The midget faded rattler (*C. v. decolor*), from certain parts of its range, is so suffused with this color as to

give the impression of a yellow snake. Specimens of the Grand Canyon rattler (*C. v. abyssus*) became almost unicolored orange when adult; and the southwestern speckled rattler (*C. m. pyrrhus*), as found in the Santa Ana Mountains of southern California, is a handsome burnt-orange snake. Patches of orange are to be seen on various other kinds of rattlers.

No rattlesnake is a brilliant red, with the pure color occasionally to be seen in other kinds of snakes, the California coral king snake (*Lampropeltis zonata*) and the Sonoran shovel-nosed snake (*Chionactis pararostris*), for examples. But many kinds of rattlers are red-brown or even brick-red, among them the red diamond (*C. r. ruber*), the Cedros Island diamond (*C. exsul*), young specimens of the Mexican west-coast rattler (*C. b. basiliscus*), the Arizona prairie rattler (*C. v. nuntius*), and western diamonds (*C. atrox*) from certain areas in New Mexico. The brightest red that I have seen on any rattlesnake was an ephemeral lateral color between blotches noted in certain specimens of the Arizona black rattler (*C. v. cerberus*) from near Hillside and Date Creek, Arizona. This color was lost immediately when the snakes were preserved. Many rattlesnakes are pink ventrally; and the southwestern speckled rattlesnake (*C. m. pyrrhus*), from some mountain chains in central Arizona and southern California, has a beautiful coral-pink or salmon dorsal color, so little marred by darker blotches that it answers the requirements of any bibulous tale. The mottled rock rattlesnake (*C. l. lepidus*) is quite pink in some areas.

Green is a common color among the rattlers, although it usually tends toward a dull olive rather than the brilliant green of some tree snakes of the tropics. The Mojave rattler (*C. s. scutulatus*), the northern blacktail (*C. m. molossus*), and some specimens of the banded rock rattler (*C. l. klauberi*) are quite green, as are the northern Pacific rattlers (*C. v. oreganus*) in the Marysville Buttes of California. All of these give the general impression of being green snakes, although other colors appear in their blotches. Olive green is a common rattler color; examples of subspecies displaying this hue are the prairie rattler (*C. v. viridis*), especially those from the upper Missouri Basin, and the adult Mexican west-coast rattlers (*C. b. basiliscus*).

No rattlesnakes are blue with the brilliance that characterizes the tails of many skinks, and few can be called blue in any sense. Some specimens of the banded rock rattler (*C. l. klauberi*) are slightly bluish, and this color is present to a lesser degree in some Arizona twin-spotted rattlers (*C. p. pricei*). Some grayish rattlers have a lavender tint; among these is the Tortuga Island diamondback (*C. tortugensis*).

The color ensembles of many rattlers involve beautiful shadings and contrasts. Among the handsomest I should place the Panamint rattler (*C. m. stephensi*) from the eastern slope of the Sierra, the Lower California rattler (*C. e. enyo*) from the Cape San Lucas region, and the northern blacktail (*C. m. molossus*), particularly specimens from the Santa Rita and Huachuca mountains of southeastern Arizona.

#### PATTERN AND COLOR AS IDENTIFYING CHARACTERS

The colors and patterns of snakes are their most obvious features and the simplest to use in distinguishing species, to whatever degree they are dependable. One entirely familiar with rattlesnake patterns, so that he has attained a certain "feel" regarding them, can readily use them in classification; but to the novice they present difficulties in application because details of pattern and color arrangement

are more important than the general color impression conveyed by the snake as a whole. Hence rattlesnake identification keys, to the extent that items of color and pattern are used, endeavor to cite particular species idiosyncrasies, in the possession of which a species may be unique, such as the vertical light line on the prenasal and first supralabial scales of the eastern diamondback (*C. adamanteus*).

In general, pattern and color are less dependable characters for classification than those of squamation, for they are more plastic and therefore variable. Pattern, especially the arrangement and contours of the light and dark marks, is more dependable than color, for the latter is the most pliable character of all. Yet even color is quite consistent in some subspecies, so that it does have some value in classification, and may even be made the basis of subspecific segregations.

Blotch shapes are not particularly useful in distinguishing species, since they are subject to much irregularity; there are often marked differences along the body of a single snake. Thus, it is often not possible to depend on distinguishing diamonds from hexagons or ellipses. In many species the posterior dorsal blotches merge with the lateral series to produce crossbands. Such species as *horridus* and *lepidus* are notable because their anterior blotches have become crossbands; and the northern blacktail (*C. m. molossus*) because the anterior blotches are often open on the sides and extend laterally as dark rows of scales that reach the ventrals. Differences as great as these from the normal rattlesnake blotches are definitely useful in diagnosis.

The nature of the light borders of the dorsal blotches is often of more importance in distinguishing species than the blotches themselves. Some species are characterized by having unicolored light scales bordering the blotches, thus making the blotch edges serrated. Example species in this category are the Mojave rattler (*C. s. scutulatus*) and the blacktail (*C. m. molossus*). In other species, the blotch edges are even, with the borders cutting across scales without regard to their presence; this is characteristic of the prairie rattler (*C. v. viridis*) and the massasauga (*S. catenatus*). In still others, the diamondbacks for example, the bordering scales are light only on their posterior tips. Blotch widths and lengths, measured in numbers of scale rows across, and in members of scales end-to-end lengthwise of the snake, are occasionally of taxonomic interest. The application of color, whether spread uniformly or in separate dots, is also important. Such species as the speckled rattler (*C. mitchelli*) and the tiger rattler (*C. tigris*) have blotches that are merely irregular concentrations of punctations.

The number of blotches on a rattlesnake—that is, the number in the main dorsal series—may be determined with a fair degree of accuracy, and may be useful in distinguishing species. True, there are sometimes doubts in counting, such as may be involved by a pair of adjacent blotches partly joined to form a single one; or instances of lateral asymmetry with more blotches on one side of the dorsum than on the other. In many Texas specimens of *C. l. lepidus*, there is a dual series of dorsal blotches of two grades, primary and secondary, and occasionally these are not readily differentiated. But, aside from such doubtful cases, the statistics of blotch counts may prove useful in distinguishing between species or subspecies of rattlesnakes. The counts of the tail rings are less satisfactory. The marks may be obscure, or partially run together, and there is often a doubt as to whether the final ring, sometimes darkening only a few of the scales that feather out over the

proximal rattle, should be counted. Since there are relatively few rings, say 5 to 10 or 12, a doubt respecting 1 or 2 is important, and for this reason statistics of tail rings are rarely useful, except in the subspecies of *C. viridis*. Sexual dimorphism is a further complication, for this materially affects the number of tail rings but not the dorsal blotches.

Elsewhere, in table 2:7, I have set forth the maximum, minimum, and average blotch counts of most of the subspecies of rattlesnakes. At this point, however, I should like to generalize upon the nature of blotch-count variations within homogeneous groups of rattlers. The curve of variation of the blotch counts is probably normal (Klauber, 1941, p. 20). There is a positive correlation between the body blotches and the tail rings, although not so high as in other kinds of blotched snakes, because the rattlesnake tail is so short (Klauber, 1945, p. 57). The coefficient of variation of the body blotches was computed for some 50 homogeneous groups of rattlers, and was found to range from 4 to 12 per cent. Most of the results fell between 5 and 8½ per cent, with an average of 6½. It was of interest to note that two of the lowest coefficients were those of island forms, the Tortuga Island diamondback (*C. tortugensis*) and the Cedros Island diamondback (*C. exsul*), both of which had coefficients of 4½ per cent. High coefficients were found in mountain species and others subject to variable ecological conditions. Tail-ring coefficients ranged from 10 to 25 per cent, many of them falling in the neighborhood of 15 to 16 per cent.

The head marks on rattlesnakes, that is, the light and dark streaks or spots, are often quite consistent and therefore useful in distinguishing species and subspecies, although some of these marks are lost as the snakes age. For example, there is the vertical light line just in front of the nostril in the eastern diamondback (*C. adamanteus*), the vertical line on the tip of the snout characterizing two subspecies of the ridge-nosed rattler (*C. willardi*), the forward-curving supraocular marks of the Lower California rattler (*C. enyo*), and the backward-curving, thin, light marks of the Mexican lance-headed rattler (*C. polystictus*). Sometimes there are differences serving to distinguish entire groups, such as the direction of the postocular light stripe that differentiates the western diamondbacks (*atrox*, *tortugensis*, *catalinensis*, *lucasensis*, *ruber*, and *exsul*) from the subspecies of the western rattlesnake (*C. viridis*); for in the former this stripe intersects the upper lip in advance of the angle of the mouth, whereas in the latter it passes rearward above the angle, as it does in the eastern diamondback (*C. adamanteus*) as well (figs. 2:141, 2:118, and 2:100).

The tail marks are moderately useful in taxonomy. Some groups, the western diamondbacks for example, are distinguished by brightly banded tails, while others, such as the timber rattler (*C. h. horridus*) and the northern blacktail (*C. m. molossus*), have unicolored tails—black in these two subspecies—with crossbands that are only faintly perceptible, if evident at all. *C. scutulatus* and *C. atrox*, although having similarly colored tails, may be distinguished by the relative widths of the black bands and gray interspaces; in *atrox* the rings and interspaces are about equal, whereas in *scutulatus* the black bands are much narrower than the gray. In a similar manner, the northern Pacific rattler (*C. v. oregonus*) may be differentiated from the southern (*C. v. helleri*), for in the former the two last dark tail rings are of equal width, whereas the final ring in the southern subspecies is about twice as wide as the penultimate.

As I have said, colors are somewhat less dependable in distinguishing kinds of rattlers than is pattern, although in some subspecies they are quite consistent. It must be recognized that the subspecies is a subjective category, and for this reason the range of the variation within a subspecies depends on the extent of the taxonomic work that has been done on a particular species. But some rattlers are so variable within a single area that color must be judged inadequate for differentiation. The southwestern speckled rattler (*C. m. pyrrhus*) is probably the most variable of all in color, for, in different areas, it is white, cream, tan, buff, drab, gray, brown, pink, orange, or salmon. Were these colors entirely consistent within areas, this form might readily be divided into many more subspecies, but there is no such consistency. This is an extreme case, but there are others, such as *C. atrox*, *C. v. viridis*, *C. v. nuntius*, *C. v. oregonus*, and *C. v. cerberus*, which show great color variations, and these not always territorially consistent.

This variability of rattlesnake colors often leads to the popular supposition that there are two or three kinds of rattlers in places where in reality only one occurs. This is particularly true in mountainous districts, where there are color differences between the snakes of the lowlands and of the higher elevations. Sometimes the pattern changes that come with age lead to the idea that there are two kinds of rattlers in the vicinity. Of course, there are many places in the United States where two or more kinds of rattlers do live in the same neighborhood—indeed, there is one area in Arizona where no less than six different species are found together—but there is a very large territory west of the Rockies and north of the latitude of San Francisco where no more than one kind of rattler occurs in any one place; yet it is quite generally believed throughout this area that different species are found at the higher and lower elevations. The following comments from some of my correspondents discuss this matter:

We have two kinds of rattlers on our range. One is the diamondback, which can be found anywhere from the Stanislaus River to the slope of the Mokelumne River; from there on to the Mokelumne River one will find the black rattler, which is not so large. *Louis Lombardi, Mokelumne Hill, Calif.*



There seem to be two different kinds of rattlesnakes in this vicinity, a large timber rattler, and a smaller snake found among rocks along streams. *Harold C. Ames, Trinity Center, Calif.*



Rattlesnakes are quite numerous in the rimrock sections of Siskiyou County, California, at an altitude of about 4,500 ft. They are locally known as sidewinders;<sup>4</sup> a small snake, seldom exceeding 30 to 36 inches, with a slender head and body. They are plentiful in the rimrocks that are numerous on the plateaus of this area, and are also found in the sagebrush flats and juniper slopes. They are timid snakes, trying hard to escape when disturbed. They rattle a lot but don't seem to mean "business" as do other varieties.

As one approaches or enters the pine-timbered slopes above the sage-juniper plateaus, he will find what is locally known as the timber rattler. This snake seems to range in the pine belt between 4,700 and 5,500 ft. They are also found at this elevation in heavy brush thickets, with fallen trees intermingled. This timber rattler is a heavy snake, growing up to four feet in length, and maybe more. It has a broad head and chunky body, and seems always on the warpath. *M. E. Barrow, U. S. Forest Service, Mt. Hebron, Calif.*



I have often wondered if we have two subspecies of rattlesnakes in this vicinity or whether we have two color phases of the same species. I have thought that the difference in coloring between the snakes of the higher and lower elevation could be due to their environments

<sup>4</sup> Not the true sidewinder (*C. cerastes*).

and the protective coloring scheme that nature has endowed them with. In any event, there appears to be quite a difference in the coloring of the snakes along the rocky banks and rims of the Rogue River and the snakes of the higher elevations which inhabit the more forested area. The snakes of the higher elevations are locally known as pine or timber rattlers, and the snakes of the lower elevations are generally called rock or spotted rattlers. *L. J. Cooper, U. S. Forest Service, Galice, Oreg.*



Although I have been told that there is only one type of rattler in this region, there appear to be three variations of the species in this district. They are chiefly described as follows: A regular gray-colored diamondback up to four and a half feet long, slender, generally not occurring at over 3,000 ft. elevation; a timber rattler, grayish-black, up to five feet long, thick up to the size of a man's forearm, ranging from 3,000 ft. to 5,800 ft. elevation; and a brown rattler having characteristic markings, slender, up to four feet long, which ranges up to 5,000 ft. elevation. *Robert Owens, U. S. Forest Service, Stehekin, Wash.*



There appear to be two species of rattlesnakes here; one a light yellowish color not particularly large; the other, much darker in color, thicker through the body, and with a blunter tail, tapering off more sharply. *N. S. Jacobson, Ryegate, Mont.*

Although there has been no corroborative evidence in the form of differences in squamation or characters, other than those of pattern and color, that would justify the conclusion that two species do exist in any of the areas discussed by these correspondents, there is no question that there are marked variations in color and pattern, probably attributable to altitude and other ecological differences. I am certainly implying no criticism of those who have assumed that these differences indicate the presence of more than a single kind of rattlesnake. Some of these differences are very marked.

#### PROCRYPsis

The fact that most snakes, rattlers included, are protectively colored, that is, are so patterned and tinted that they are with difficulty distinguished from their backgrounds, is well known. As long ago as the second century B.C., Nicander (translation of 1953, p. 39) stated that some snakes adopt the color of the ground on which they live. I have pointed out elsewhere (p. 460) that the effort to avoid discovery by depending on concealing coloration is the first step, although an inactive one, in the rattlesnake's normal defensive program. That it is often highly effective cannot be doubted.

Rattlesnakes of particular species live in too many differing environments to be dependent entirely on color matching for concealment; for what might blend with the background in one place might prove conspicuous in another. But even so, many startling examples of the likeness of a snake's color to its most usual surroundings are to be noted. In addition, the principle of disruptive coloration (Cott, 1940, pp. 48, 58, 67) is obviously involved in the dark dorsal blotches characteristic of most rattlesnakes. The writer (1931b, p. 43) pointed out that active snakes tend to be unicolored or striped, whereas those that are heavy-bodied and slow-moving are usually blotched. The rattlesnakes fall in the latter category. Even the lateral patterns of the heads, and the color of the iris itself, are successful in making the eye less conspicuous (see Cott, 1940, p. 85). One might suppose that if there were any validity in the myth of the rattlesnake's power of fascination, the pattern would be such as to render the eye more, rather than less, conspicuous.

The darkest rattlesnakes are usually found in the areas of heaviest rainfall and densest shrubbery cover, whereas the lightest are found in the most arid territories. Examples of the first group are the eastern diamond rattler (*C. adamanteus*) of Florida and the Southeastern states; the timber rattler (*C. h. horridus*) of the Northeast; the eastern massasauga (*S. c. catenatus*); and the black rattler (*C. v. cerberus*) of central Arizona. The little rattlers of the high altitudes of Mexico, *C. triseriatus* and *C. intermedius* and their subspecies, as well as *C. pusillus*, *C. transversus*, and *S. rarus*, are notably dark. In an opposite class we may list the sidewinder (*C. cerastes*) of the desert sands, and the Great Basin rattler (*C. v. lutosus*) and midget faded rattlesnake (*C. v. decolor*) of the arid intermountain section.

Where a kind of rattlesnake is restricted to an area of relatively uniform background with which the color of the snake matches, there is a tendency toward a reduction in the size or contrast of the spots—that is, a trend toward concealment by matching rather than disruptive coloration, examples of which are the Grand Canyon rattler (*C. v. abyssus*) and the southwestern speckled rattler (*C. m. pyrrhus*).

That there is in some degree a matching of rattlesnake hues with their normal backgrounds there can be no doubt; this is particularly evident if we survey pattern trends within a species. For example, the western diamond (*C. atrox*) becomes lighter, more clay-colored, and with less conspicuous blotches as we pass westward from Texas into more arid areas where bare soil or rock predominates. As one goes south from Montana and the Dakotas, the prairie rattler (*C. v. viridis*) becomes less green and more yellowish or brown, until, when the Painted Desert in Arizona is reached, it has become reddish and matches the soil there—it is, in this area, considered a separate subspecies, the Arizona prairie rattler (*C. v. nuntius*). Westward toward Flagstaff, where the vegetative cover is heavier, it again becomes greenish, with more conspicuous markings.

Throughout California, the Pacific rattlers (*C. v. oreganus* and *C. v. helleri*) are considerably darker in the mountains than in the lowlands. There is a particularly light color-phase of *oreganus* in the arid west side of the San Joaquin Valley. The Great Basin rattler (*C. v. lutosus*) tends to lose the dark brown in the centers of the dorsal blotches in its more arid and barren habitats. The sidewinders (*C. c. cerastes* and *C. c. laterorepens*) adhere to the hues of the desert sands on which they live, pink in some areas, buff or gray in others. In the mountains of southern Arizona there is a notable parallelism in the gray-blue ground color—but not in the blotch patterns—of the two little rattlers that match the rocks of their habitats, the banded rock rattler (*C. l. klauberi*) and the Arizona twin-spotted rattler (*C. p. pricei*).

On El Muerto Island, Charles H. Lowe, Jr., found the little speckled rattlers (*C. m. muertensis*) difficult to see, although the rocks among which they were found were multicolored. Fitch (1949a, p. 518) has pointed out how hard it is to discover rattlers (*C. v. oreganus*) on the San Joaquin Experimental Range, so perfect is their concealing coloration. Lewis (1949, p. 183) has mentioned finding two unusually dark blacktails (*C. m. molossus*) amid black lava. Smart (1951, p. 45) made color analyses and found a high degree of correlation between the colors of *C. v. lutosus* at a den near Salt Lake City and the soil and vegetation roundabout.

But with all this obvious matching there are some colors that are difficult to explain. The red diamond (*C. r. ruber*) of southern California is such an example. For, although it matches some of the soils and rocks on which it lives—especially on

the desert side of the mountains, where, incidentally, it is lighter in color, with many white scales on the sides—it is highly conspicuous amid the granite boulders and the green cacti that it seems to prefer in the coastal foothills. But this is a notable exception, for, by and large, rattlesnakes, through a combination of blending, and of disruptive colors and patterns, are usually difficult to detect when motionless.

Color may be important, not only as an aid to procrypsis, but also in its effect on radiation reflectivity. That is, desert species may be light colored, not only to match their barren backgrounds, but also to reduce heat absorption. Elsewhere (Klauber, 1939a, p. 78) I have stated the conclusion that under conditions where protective coloration and protective reflectivity work to the same end, their effects on color are cumulative and important. Where they are at cross-purposes, protective coloration is usually controlling. An example of a situation of the latter character is that of a black lava desert. Here, for procrypsis, the reptiles should be dark, but to reduce radiation absorption they should be light colored. Under these conflicting objectives, the indigenous reptiles, particularly those that are largely diurnal, are generally dark. It is to be remembered that the color of a creature is only an indication of relative reflectivity in the visual band of the spectrum; the average reflectivity over the entire range of wave lengths of the incipient radiation may not differ so greatly as would be suggested by the visual colors alone. A recent discussion of some of these radiation problems is that of Kelly, Bond, and Heitman (1954, p. 563).

#### PHYSIOLOGICAL COLOR CHANGES

Snakes, rattlesnakes among others, have some power of color change, although only to a small degree compared with that possessed by many lizards. I have reported this (1930a, p. 131; 1931b, p. 46; 1939a, pp. 76, 77) in sidewinders (*C. cerastes*), southern Pacific rattlers (*C. v. helleri*), and Arizona black rattlers (*C. v. cerberus*). The change involves a lightening of some areas with increased temperatures, particularly the dorsal areas between blotches. Subsequently Rahn (1942, p. 178) verified the effect of temperature on the prairie rattlesnake (*C. v. viridis*); he showed that higher temperatures caused a lightening of the color by contracting the melanophores. At lower temperatures the pigment disperses, thus making the dark color on the surface more apparent. Rahn had previously shown (1941, p. 228) that the removal of the pituitary causes a permanent paling of *viridis* through concentration of the melanophore pigment. The paling is more evident after the shedding of the old keratinized epidermal layer. Rahn's results have been discussed by G. H. Parker (1948, p. 210).

But these slight color changes induced by temperature, which can be detected only by the most careful comparisons with controls not subjected to the same temperature differences, are not to be taken as verifying the remarkable differences in color and pattern attributed to anger and other stimuli, as ascribed to rattlers by some of the early travelers (see also p. 475). Carver (1778, p. 480) stated that the snake's colors flashed more beautifully when the creature was animated by resentment. Weld (1800, p. 409; also Warburton, 1849, p. 175, and Browning, 1860, p. 378) reported that the skin took on a different color when the snake was wounded or enraged. Bingley (1803, vol. 3, p. 74) wrote that a rattler lost its beautiful pattern

after biting itself. Meek (1946, p. 105), a modern purveyor of myths, said a man watching a diamondback saw it change color until it had exhausted the rainbow. I have subjected a large number of rattlers to a variety of tests that might have been expected to induce great color changes, if any of these stories of the effects of rage and other stimuli were true. No such changes were observed, even following decapitation. These supposed extensive color changes are mythical, the results of campfire tales, or observations by travelers too excited by the presence of a rattler to be accurate judges of hue and tone.

#### ONTOGENETIC CHANGES

In most subspecies of rattlesnakes, the young are more clearly and brightly patterned than the adults, with the light and dark marks more sharply contrasted in the juveniles. This is true, for example, of the black-tailed rattler (*C. molossus*), the Mojave (*C. s. scutulatus*), and the various subspecies of the western rattlesnake (*C. viridis*). Some subspecies almost entirely lose their marks with age; among these is the Grand Canyon rattler (*C. v. abyssus*), which has conspicuous blotches when young but becomes an almost uniform orange color with age. Another species that tends to lose its marks with age is the Aruba Island rattler (*C. unicolor*). Rattlers having melanistic phases may be blotched when young, yet almost solid black when adults. This is to be observed, in some areas, in the timber rattler (*C. h. horridus*) and the eastern massasauga (*S. c. catenatus*). The secondary blotches interspersed between the primary series in *klauberi* become relatively less conspicuous with age.

The ontogenetic loss of body blotches is often duplicated by the obliteration of characteristic head marks as well. This is the case in the southern Pacific rattler (*C. v. helleri*), which has marks on the top of the head that completely disappear with age. In the northern Pacific rattler (*C. v. oreganus*) this loss is particularly evident on the sides of the head, where both pattern and color, below the pit and at the angle of the mouth, disappear, leaving a characteristic white-faced appearance. This is especially to be noted in specimens from the Coast Range in northwestern California.

Changes in tail patterns also occur, but less conspicuously than in the case of the head marks. Several kinds of rattlers are born with bright-yellow tails, among them the pigmy rattler (*S. miliarius*), the banded rock rattler (*C. l. klauberi*), and the southern Pacific rattler (*C. v. helleri*). In *klauberi* the tails become salmon-red with age; the others become gray, and sometimes, in *helleri*, black. The possible utility of the bright-yellow tails of the juveniles in attracting prey has been discussed elsewhere (p. 662). Usually pattern changes in the tails of rattlers involve a loss of definition in the tail rings.

Coincident with pattern changes, there are often color changes, as well. Many kinds of rattlers, probably most of them, tend to darken with age. An example of this kind of change is to be found in the southern Pacific rattler (*C. v. helleri*), which becomes considerably darker as it grows; especially is this true of mountain specimens. The Aruba Island rattler (*C. unicolor*), on the other hand, becomes lighter with age, as does the red diamond (*C. r. ruber*). Unborn young of the latter subspecies are almost black; at birth they are dark red-brown, subsequently changing to red-brown or even brick-red. Sometimes there is a change of hue; the Mexi-

can west-coast rattler (*C. b. basiliscus*) is reddish when young but becomes greenish or olive-green when adult. In general, it would appear that procrypsis by disruptive coloration is paramount in the young, and by matching in adults.

As might be expected, the skin-shedding process results in a brightening of the color and pattern. Although a skin ready for shedding has little color, through surface wear and the accretion of foreign matter it loses some of its transparency, and the keratin of which it is composed has a natural straw color. Thus, upon its removal, the snake's pattern shows with renewed brilliancy.

#### SEXUAL DIMORPHISM

Sexual dimorphism in pattern and color is not important among the rattlesnakes. It is most evident in the timber and canebrake rattlers (*C. h. horridus* and *C. h. atricaudatus*). In these subspecies yellowish specimens are nearly always females, whereas the black specimens are generally males, as discussed elsewhere (p. 665). Various other sexual pattern-differences have been ascribed to the rattlesnakes, especially to *horridus* and its subspecies. It has often been said that certain marks on the head distinguish the males from the females, but this has been found to be without basis. It has been believed that the males of the eastern diamondback (*C. adamanteus*) have diamond-shaped blotches and the females heart-shaped ones (Adair and Ewbank, 1922, p. 356). No such difference can be verified. As to numbers of blotches, there are no significant differences between the sexes with respect to the body blotches; but because of the greater length of the tails of the males compared with the females, the former have a correspondingly greater number of tail rings.

#### EFFECT OF ULTRAVIOLET LIGHT

Atkins (1948, p. 511) has reported that rattlers and copperheads fluoresce to a bright green under ultraviolet light. On the chance that such fluorescence might bring out pattern differences not evident under normal lighting, I tested a number of rattlesnake subspecies, including *ruber*, *helleri*, *lutosus*, *cerastes*, and *laterorepens*. No fluorescence could be detected, that is, no illumination not attributable to the small amount of light in the visible range that such lamps emit. Thus I was unable to verify Atkins' statement, as far as rattlers were concerned. Rattlesnake rattles do have a slight fluorescence, usually yellowish. The fangs fluoresce brightly, with a light-green color. The upper parts of the fangs are more fluorescent than the points; also, the fangs are more fluorescent than the other bones of the skull. Dried venom does not fluoresce.

#### FREAKS AND ABERRANTS

Various kinds of freakish or aberrant rattlesnakes are occasionally seen. Some are abnormal in form; of these, two-headed snakes are the most interesting to the public. Others have various defects, many of which are such as to prove lethal at birth or shortly thereafter. Hybrid rattlers also occur, more often in captivity than in nature. Abnormalities are commoner in pattern and color than in form.

In color they range all the way from albinism to melanism. The most notable pattern aberrancy is the substitution of longitudinal stripes for the blotches or crossbars that characterize most rattlers.

#### TWO-HEADED SNAKES

Two-headed snakes are freaks or monsters that occur as a very small percentage of normal births, just as they do among most other kinds of animals. As they are usually defective anatomically, they rarely survive beyond a few days after birth. Although two-headed snakes have long been known—they were even discussed by Aristotle (Peck, 1943, p. 423)—the early accounts were elaborated into, or confused with, various mythical creatures described in the early natural histories, such as the seven-headed hydra (Gesner, 1587, fol. 63r; Topsell, 1608, p. 201; Aldrovandus, 1640, pp. 387–88, Jonstonus, 1657, plate 10). What may be the earliest illustration of a real multiple-headed snake (a three-headed exaggeration of a two-headed one) is that of Von Caub (1517, *De Animalibus*, chapter 60—the pages are unnumbered). The creature illustrated by Aldrovandus (1640, p. 60; Jonstonus, 1657, plate 1) is certainly a real two-headed snake rather than a mythical creature.

In some instances, bicephalous snakes have been considered by the early naturalists to be distinct species, that is, a particular kind of snake of which all individuals were presumed to be two-headed. But there were dissenters from this view from the earliest times; Aristotle himself recognized that they were only rare, freakish representatives of common species, and the theory that there are races of two-headed snakes long ago lost its adherents.

Another confusion, however, that persists to the present date, results from the application of the unfortunate term "two-headed" to various narrow-headed, blunt-tailed snakes, owing to a fancied similarity of their heads and tails. For example, the little boas found in the western United States—the California boa (*Lichanura roseofusca*) and the rubber snake (*Charina bottae*)—are sometimes called two-headed snakes, because at a distance one might take the tail to be the head. Needless to say there are no snakes with a head at each end. One spectator at the San Diego Zoo was heard to decry the attention given a live two-headed king snake; he thought it unworthy of notice since both heads were at the same end.

Some recent publications on two-headed snakes are those of Roswell H. Johnson (1902, p. 523), Cunningham (1937), Nakamura (1938, p. 171), and Hamburger (1947, p. 666). Johnson presented a complete list of the specimens known up to 1902. Cunningham, in a book devoted entirely to two-headed snakes, made an extensive survey of the literature, redescribing and picturing every specimen of which he could find a record. Nakamura's contribution proposed an elaborate system of classification, based on the degrees of separation of the two heads and necks. Hamburger discusses the formation of these monsters, with the conclusion that they represent incomplete identical, rather than fraternal, twins (p. 674). He also mentions experiments on their artificial formation (p. 675), which indicate that two-headedness may result from a mechanical restriction or pressure on the egg during development.

I have few numerical data as to the frequency with which two-headed snakes occur, but the percentage must be quite small. W. A. King, of Texas, one of the largest commercial snake dealers in the country, informed me that no two-headed

rattlesnakes had been brought in by his field collectors. E. Ross Allen, of Silver Springs, Florida, secured one specimen among about 50,000 normal rattlesnakes that he bought or collected. During the past 30 years some 20,000 snakes, of more than 30 subspecies, have been recorded in a species census of snakes from San Diego County, California, and there was a single two-headed individual (a king snake) among them. But such statistics are hardly to be taken as a conclusive indication of the frequency with which bicephalous individuals occur, because these freaks seldom survive their births for very long, and such live ones as are found are discovered through the lucky chance of coming upon them immediately after birth. A major proportion of the known specimens belong to species that give birth to their young alive (ovoviviparous), and were taken from the mothers as unborn embryos. Of the oviparous (egg-laying) species, most of the known two-headed specimens were found alive, since snake egg clutches are seldom discovered just before they hatch. The data are too meager to determine whether two-headed snakes occur more often in oviparous than in ovoviviparous species.

I have not been so fortunate as to have seen a live two-headed rattlesnake; the only two living freaks of this kind to which I have had access were a small garter snake from Oregon, and a king snake from San Diego County. Each had two well-developed heads. The garter snake was said to drink with either head, but would feed through only one—at least, so its owner reported. I watched it crawl and observed that the heads apparently struggled for control of the body, with the result that there was little or no purposeful movement, until one head became tired and hung rather limply, whereupon the other would take control and the snake would crawl quite normally, with the guiding head directly before the body, and the other trailing dispiritedly at the side. The king snake, which is still thriving as this is written, eats and drinks with both heads, although one is slightly less spirited than the other. Unless restrained, both heads will seize and endeavor to eat the same mouse. The snake has been in captivity for two years and has made a considerable gain in size. It was evidently not long out of the egg when caught.

I now present, in chronological order, a summary of such published accounts describing two-headed rattlesnakes as I have come upon in the course of this study. Rattlers are ovoviviparous, and a number of those reported were embryos removed from the mother. I have no absolutely trustworthy record of any specimen that was more than a few weeks old at most. I do not know of any two-headed rattler with the degree of separation between the heads, and their perfect formation, that characterized a milk snake (*Lampropeltis doliata*) which lived for several months at the New York Zoo (Hyde, 1925, photograph, p. 186). Many of the two-headed rattlers described had heads so distorted that even a live birth must be considered doubtful, although several days, or even weeks, of life undoubtedly occurred in some of the cases listed hereunder. It should be understood that in most two-headed snakes of whatever species, the heads are not completely separated, on separate necks, but rather are fused together along the side, often between the eye and the angle of the jaw. The bicephalous snake with two distinct and perfectly formed heads is a rarity among rarities.

Baird (1856, p. 60) mentions the acquisition of a double-headed rattler secured by Lieut. T. E. Patterson at Camp Yuma, California, and presented to the Smithsonian Institution. No further information on the specimen is available. Since it

was not listed by Yarrow (1883b), in his catalogue of the herpetological material in the museum, it is presumed to have disappeared from the collection before that date.

Michler (1857, p. 121) tells of the removal, from a mother snake, of a set of embryos, one of which was bicephalic. Michler's statement is contained in the report of the Mexican Boundary Survey (Emory). The parent rattler was collected by Dr. Robert J. Abbott in the Sierra del Pozo Verde, southern Arizona. The two heads were said to be perfect. The species was not designated. There is a strong probability that the specimens mentioned by Baird and Michler were one and the same. Both Lieut. Patterson's and Dr. Abbott's specimens were forwarded to the Smithsonian from Camp (or Fort) Yuma, and both men were connected with the Mexican Boundary Survey.

Anon. (1877, p. 105) calls attention to an article in the Mount Sterling, Pennsylvania, *Democrat* which mentioned the killing of a large rattler that had two well-developed heads on necks about four inches long. Were it possible to verify this report—an adult rattler with heads so well separated—this would constitute the most mature and perfect specimen of a two-headed rattler ever reported. In view of the frequency of newspaper exaggerations and hoaxes, the story must be considered doubtful.

Levering (1878, p. 194) records a juvenile twin-headed rattler plowed up by Capt. Charles McNeal at Greenwood, Jackson County, Missouri. It was a foot long. Allen Kelly (K., A., 1909b, p. 691) shows an excellent photograph of a young two-headed rattler, killed near Yuma, Arizona. The two heads were joined at about the angle of the jaw. I judge from the picture that the snake was a Mojave rattler (*C. s. scutulatus*).

Raymond L. Ditmars seems to have had three bicephalous rattlers at the Bronx Zoo at different times. While not described in his own publications, they are mentioned by Hyde (1925, p. 187) and Cunningham (1937, pp. 30, 31.) One had one head that had functional eyes and tongue, but the other head had a sealed mouth. The second snake had active tongues and well-formed eyes in each head. The third was bifurcated at the eye level, forming a broad head with only two eyes.

Amaral (1926b, p. 101) shows a photograph of a young bicephalous South American rattler (*C. d. terrificus*) collected at Aracatuba, state of São Paulo, Brazil. The snake had the two heads joined at about the last supralabials, some 25 mm. back of the snout. The total length of the specimen was 281 mm. The rattle is apparently in the button stage, rather than the prebutton stage, so the snake may have lived 10 days or so after birth, long enough to shed its skin once.

The newspapers of mid-January, 1926, contained a widely syndicated article concerning a two-headed rattlesnake collected by C. H. Bridge between Prather and Auberry, Fresno County, California. An excellent photograph of this snake appeared in the *Fresno Morning Republican* of January 12, 1926 (p. 7, cols. 6–7). It shows the snake to be in the prebutton stage and therefore not over 10 days old, if it lived that long. Some of the accounts in the press referred to it as being from three months to a year old. As a matter of fact, the catalogue entry at Fresno State College, where the specimen is now, refers to it as having been removed from the mother when she was killed, although this was not mentioned in the original newspaper accounts. I have examined this specimen and found an interesting divergence

in the head scales of the two heads. The supralabials were 14–15, 15–15; and the infralabials 17–16, 15–15. The canthals were 2–2, 2–3; and the scales between the supraoculars 5 + 5, 3 + 5. In each instance I have given the counts on the right-hand head first, and, where there are two counts per head, the right side of the head first. The specimen is 227 mm. over-all—small for a northern Pacific rattlesnake (*C. v. oreganus*) at birth. The heads are fused just behind the angles of the mouths and are more in opposition than is usually the case, the angle between them being about 160 degrees. This snake is a female.

Mrs. Grace Olive Wiley (1930, p. 101) reported finding a two-headed male embryo among a brood of 47 removed from a Mexican west-coast rattler (*C. b. basiliscus*) that died in captivity. The heads were joined near the eyes. There were four eyes, but the inner ones were in contact. Behind the eyes the mouth was single. There was one trachea with two tongues, side-by-side. The pits, nostrils, and fangs were normal.

On December 1, 1933, or 1934, certain newspapers carried a report from Idabel, Oklahoma, concerning a bicephalous rattler collected by Troy Proctor, four miles west of Broken Bow, McCurtain County, Oklahoma. It was stated to have had two distinct heads, with two tongues, and four eyes. The heads could be used separately or together. The snake was reputed to be half-grown, which, of course, lacks confirmation.

Cunningham (1937, p. 60) reports having received the anterior section of a two-headed rattler from Clarence Nading of Elkport, Iowa. Fusion was at the base of the head. The species of the snake is not given. H. E. Miller (1938, p. 17) makes this statement without further elaboration: "We have a record of at least one two-headed rattler that seized food with both heads, there sometimes being a disagreement between the two heads of the one serpent."

Vanzolini (1947, p. 273) describes very fully a two-headed South American rattler (*C. d. terrificus*) from the state of Matto Grosso, Brazil. It is a small snake in the prebutton stage and only 150 mm. long—much shorter than a full-term juvenile of this subspecies. It may, therefore, have been removed from the mother before birth, although not very long before, as the pattern is well developed. The heads are better separated—one has a complete neck—than in any other bicephalous rattler of which I have seen photographs; but behind the first point of fusion, there is a considerable protuberance with distortion and twisting of the body halves, as if the entire structure were abnormal. Vanzolini found scale differences between the heads, similar to those in the Fresno County specimen, from which he draws the conclusion that this is a case of the merging of fraternal, rather than of identical, twins.

The finding of a two-headed timber rattlesnake (*C. h. horridus*) near Logan, West Virginia, was reported in 1947 ([Rimkus], p. 23). This snake was said to have been captured alive. Through the courtesy of Joseph Rimkus of the Logan *Banner*, I am able to present a photograph of this snake (fig. 4:2). The heads are seen to be well formed, with the point of fusion posterior to the angle of the mouth. The snake was stated to have had the use of both tongues. Neither the scales nor the patterns of the two heads match exactly.

Mrs. Madge V. Ratcliffe, a commercial dealer of Medicine Hat, Alberta, Canada, informed me in 1949 of a two-headed prairie rattlesnake (*C. v. viridis*), one of a

brood born in her cages. This freak was most unusual in that the heads and necks were separated for about three inches; then followed a single trunk about four inches long, with the tail sections again separated for some three inches. She said the little snake was incapable of coiling or locomotion, but the heads moved freely and independently. This is the only bicephalous rattler of which I have heard, with separate heads, necks, and tails—classified by Nakamura (1938, p. 172) as “tera-



Fig. 4:2. Two-headed timber rattlesnake (*C. h. horridus*). (Preserved specimen from Logan, West Virginia. Photographed through the courtesy of Joseph Rimkus.)

topagus, anakatamesodidymus”—although the literature contains mention of a number of snakes of other kinds having this type of division.

In November, 1953, Ross Allen, owner of the Reptile Institute, Silver Springs, Florida, received a two-headed eastern diamondback (*C. adamanteus*) that had been collected by J. C. Sharp, near his home at Odessa, Florida. This snake lived long enough to shed the prebutton. The heads were joined at the eye, and one was quite imperfect.

It should be stated, with regard to these two-headed freaks, that the popular interest in them exceeds the scientific. When people find such a creature, they are likely to have quite fantastic ideas concerning its value. If such a snake could be

kept alive for awhile, it might be worth something to a roadside snake show, but to any scientific institution it would have only a passing interest and a purely nominal value.

Experiments with artificial twinning in amphibians lead to the conclusion that identical and not fraternal twinning is involved in bicephalous snakes, notwithstanding the scale differences that have been observed in the two heads of a pair.

#### DEFECTIVE YOUNG

I have elsewhere commented on the frequency with which defective young occur in broods of rattlesnakes born in captivity (1936b, p. 19; 1945, pp. 84, 89, 91; also p. 730 in this work). I do not know whether they occur more often in the case of captive mothers than in the wild. Some are so deformed that they obviously would not survive, as, for example, snakes without eyes, with malformed heads, or twisted bodies. Adhesions between two parts of the ventral surfaces are sometimes noted. Occasionally these defects run in families. In two successive broods from the same red diamond rattlesnake (*C. r. ruber*) parents, nine eggs in each brood failed to mature. The first brood also contained three born before full term, one apparently normal but born dead, one with a defective eye, and two normal. The second brood included one born dead, one without a left eye, one with an exceedingly small and obviously inadequate head, and eight normal or apparently so.

Yet the aberrancies observed in broods are not always lethal. In another brood of the same species, 8 young out of 11 had the first infralabial scales fused to the mental, a characteristic not present in the mother, and of exceedingly rare occurrence in this or any other species of rattlesnake. Occasional deviations of scales from the normal, either in arrangement or number, have been observed in adult specimens captured in the wild. For example, I have seen a specimen of the northern Pacific rattler (*C. v. oreganus*) with 33 scale rows, although the average in this subspecies is 25.4, and specimens with as many as 29 comprise less than one per cent of the population. We have had at the San Diego Zoo a strain of pine snakes (*Pituophis m. melanoleucus*) that has produced an exceedingly high proportion of defectives of several kinds, blindness being frequent.

#### ALBINISM

Albinism, a pigment deficiency, has been noted from time to time in practically all animals of which adequate series have been observed. It is not a particularly rare phenomenon. Once occurring, it is likely to be most persistent in inbred populations. For example, the Hopi Indians of northern Arizona are characterized by a relatively high percentage of albinos (Klauber, 1932a, p. 15). George Shiras (1921, p. 182) has called attention to the prevalence of albino deer on Grand Island in Lake Superior. Albinism has been shown to be a Mendelian recessive character, which accounts for its accentuation through inbreeding. At the San Diego Zoo, C. B. Perkins has been able to develop, through back-crossing from a single albino female, a pure strain of albino San Diegan gopher snakes (*Pituophis catenifer annectens*). The albino offspring, in the first generation, were produced in approximately the proportions to be expected for simple recessives.

In wide-ranging populations, albinism probably occurs to the extent of one-tenth to one-hundredth of one per cent of the population. Perkins, raiding dens

of the prairie rattlesnake (*C. v. viridis*) at Platteville, Colorado, secured one albino specimen out of about 850 rattlers collected. This was a juvenile (fig. 4:3). At the San Diego Zoo we have had seven wild albinos—three gopher snakes, two California king snakes, a California boa, and a leaf-nose—out of some 20,000 snake specimens recorded from San Diego County. Although about 4,000 rattlesnakes were included in this census there were no albinos among them.

Albino snakes probably suffer in competition with their normal fellows: their eyesight is perhaps defective, as is the case with most albinos, and they lack protec-



Fig. 4:3. Juvenile albino prairie rattlesnake (*C. v. viridis*) compared with one of normal coloration. (Specimens from near Platteville, Weld County, Colorado.)

tive coloration, making them more readily subject to predation. Hence, most albino snakes found in the wild are juveniles, although this is not invariably the case, as it is with two-headed snakes, for the latter almost always suffer from serious anatomic aberrations in addition to bicephalism, and albinos do not.

A completely albinistic rattlesnake has pink eyes and lacks all of the darker colors usually evident in the normal pattern of the species to which it belongs. Yet the pattern may still be faintly discerned, because the pink of the tissue within is more evident through the patches of skin normally dark, than through those normally straw color, which color, indeed, is to some extent retained. In other words, there is a retention of opacity in the normally light areas not evident in those normally dark, which areas are seen to be somewhat transparent.

It is generally agreed that albinism has little or no effect on evolution; light-colored species are not derived from an albino ancestry. Thus, the Aruba Island rattlesnake (*C. unicolor*), a conspicuously light species allied to the Neotropical rattlesnake (*C. durissus*), is in no way a result of albinism; nor are the almost white specimens of the southwestern speckled rattlesnake (*C. m. pyrrhus*) found in the

Tinajas Altas Mountains of southern Arizona albinistic. Such scattered spots as this white *pyrrhus* retains are quite dark, and the eyes are dark.

Albinos are sometimes taxonomically confusing, but there is no instance of a supposed new species of rattlesnake based on an albino. Although Amaral (1926a, p. 56) presumed that the type specimen of *Crotalus pulvis* Ditmars, 1905, was merely an albinistic *C. durissus*, the weight of the evidence now indicates that it was a specimen of *unicolor*, as concluded by Gloyd (1940, p. 141). There is no certainty that the specimen came from Nicaragua, as supposed, for it passed through several hands before reaching Ditmars. The scale counts fit *unicolor*, but do not fit *durissus*, *terrificus*, or any other mainland rattler of this group. *C. unicolor*, by the way, is relatively much lighter as an adult than as a juvenile. This, however, does not justify the idea expressed in Japanese folklore (Opler, 1945, p. 258) that white snakes are very old, a belief that was used by Kipling in the story of "The King's Ankus," wherein a cobra guarding a treasure was so old that it had turned completely white. It is not a universal rule by any means that snakes which change their patterns as they age tend to lighten. Highland specimens of the southern Pacific rattlesnake (*C. v. helleri*) and the Arizona black rattlesnake (*C. v. cerberus*) grow conspicuously darker as they age.

A number of albino rattlesnakes have been mentioned in published accounts. Comancho (1893, p. 316) described an albino prairie rattler (*C. v. viridis*) from 12 miles east of Beatrice, Nebraska. This report initiated comments by correspondents in *Forest and Stream*, one of whom suggested that the light color might be incident to some chronological phase of skin changing. To this Comancho replied that the snake was still alive and the color had not changed, despite shedding. The correspondence also brought forth a report of another albino rattler (Savage, 1893, p. 492) from southwestern Texas. The species was not named.

Ditmars (1921, p. 131) pictures a young albino timber rattler (*C. h. horridus*) that was collected at Black Rock, Mt. Everett, Massachusetts. A second specimen, thought to be a year older, was taken on the same rock ledge a year later (Ditmars, 1923, pp. 49, 115). This is the only instance known to me of two albino rattlers, possibly belonging to the same brood, captured at the same locality. A photograph of the first of these individuals has often been reprinted (Ditmars, 1921, p. 131; *Illustrated London News*, Sept. 13, 1924, p. 497; Ditmars, 1929, p. 119; 1935, fig. 29).

Babcock (1925, p. 5) mentions a New England albino *horridus* from Black Rock, Mt. Washington, near Pittsfield, Massachusetts, which I presume to be the same locality as Ditmars' Black Rock, so that this record may possibly be based on one of the foregoing specimens. Miller (1938, p. 17) also mentions albinos of this subspecies, but without being specific as to the specimens he has seen.

A number of albino South American rattlers from Brazil have been recorded. Amaral (1926a, p. 55) mentions three from San Roque, Itú, and Rio Pardo, all in the state of São Paulo; and later (1932, p. 83) he reported another from Ipaussú in the same state. Prado and de Barros (1940, p. 31) list two more albinos of this subspecies, one from Palmar, also in São Paulo, the other from Barra Bonita, Santa Catarina. It is interesting to note that all six of these specimens were adults (810 to 1,035 mm. in length), and that both sexes were represented. Renault and Schreiber (1949, p. 91) mention a young albino from Divinópolis, Minas Geraes, Brazil; and Hoge (1952, p. 269) two from Japira, Paraná, that had not progressed beyond the button stage.

I have two albino rattlesnakes preserved in my collection, and have seen two others. One of mine is a juvenile female prairie rattler (*C. v. viridis*), already mentioned, from Platteville, Colorado. The other is a young male of the same species from 20 miles north of Quinn, Pennington County, South Dakota. This was sent me by W. B. Harvey, who also lent me, for examination, another albino, a three-rattle female from 30 miles northwest of Wall, in the same county. The blotches were visible as pinkish saddles on a white background. The rattle was pure white. The eyes were pink in life. Cornell University has a two-rattle northern Pacific rattler (*C. v. oregonus*), a male, from the mouth of Los Gatos Canyon, near Coalinga, Fresno County, California. This is an almost perfect albino, although there are six light-brown spots visible anteriorly and two near the tail. The rattles are white.

#### MELANISM

Melanism—the occurrence of black individuals—seems to be of two kinds. The first involves the continued presence of many black, or almost black, individuals in a population otherwise not distinguished by being conspicuously darker than neighboring populations that do not produce melanos. This type of melanism is usually ontogenetic, for the individuals destined to be black as adults are normally colored at birth. The second type involves only a very few specimens, and may, like albinism, be the result of some chance genetic disturbance that may appear in one or several individuals and then be eliminated from a population.

Among the rattlesnakes, the first kind of melanism occurs among the eastern massasaugas (*Sistrurus c. catenatus*). These rattlesnakes ordinarily are quite dark-colored, but with a conspicuous pattern of squarish brown or black blotches on a gray-brown ground color. In some areas, however, many individuals are uniformly black (fig. 4:4), although the pattern is sometimes faintly evident in different densities of black, a difference accentuated upon preservation in alcohol. Conant (1938, p. 113; 1951, p. 254) points out that the black specimens have light areas on the underside of the head and neck. He states that the young—including those born to melanistic mothers—are normally colored; thus the effect is ontogenetic. Of 14 collected near Mt. Victory, Hardin County, Ohio, all adults were black and all juveniles spotted. In other Ohio areas black specimens are less common. Gloyd (1940, p. 54) calls attention to melanistic specimens from Indiana, Illinois, Wisconsin, and Michigan. Roberts and Quarters (1947, p. 6) found one black specimen among 10 collected in Michigan. There is no evidence that this diffusion of ontogenetic melanism within this rattlesnake subspecies is in any way ephemeral. Kirtland described a black specimen as a possible new species (*massasaugus*) as early as 1838 (p. 190). Specimens of the Mexican pigmy rattlesnake (*S. ravus*) are also occasionally melanotic.

Another rattlesnake having a melanistic strain is the timber rattlesnake (*C. h. horridus*), of which black individuals are moderately common in the eastern part of the range, particularly at the higher elevations (Ditmars, 1929, p. 111; 1935, p. 32; Gloyd, 1940, p. 184). Usually the pattern is evident to some degree, especially posteriorly, but some individuals are uniformly black. Most of the black specimens are males; however, it is not true that they are invariably males, or that all males are black, as was once thought to be the case.

These are instances of melanism of the first type, wherein rather widespread populations continually manifest a black phase. The other type is that in which only one or a very few melanistic individuals occasionally appear in an otherwise normally colored population. Stearns (1877, p. 623) mentions a jet-black rattler, "without even a white shade on the belly," taken near Niles, Alameda County, California. Mrs. Margaret Darrell advised me of seeing "coal black rattlers, their markings barely distinguishable," at Eagle Rock Lookout, Santa Cruz County, California. At both of these places normally colored rattlesnakes—they are north-



Fig. 4:4. Melanistic eastern massasauga (*S. c. catenatus*).  
(Adult female, probably from Ohio.)

ern Pacifics (*C. v. oreganus*)—are gray or greenish, with brown or black blotches.

In 1930, W. A. Bevan wrote me of the occurrence of melanistic specimens of the prairie rattlesnake (*C. v. viridis*) west of Fort Collins, Colorado. He had seen one specimen that was quite black and had heard of others. Gloyd (1935, p. 665) mentions another specimen of the prairie rattlesnake (*C. v. viridis*) seen near Spearfish, South Dakota, that had sufficient black pigment to obscure the pattern almost completely. I have not been fortunate enough to see any representatives of this sporadic type of melanism, nor is it known whether it develops ontogenetically. Such specimens are apparently more of the character of true freaks than the melanistic individuals that represent a color phase among the massasaugas and timber rattlers.

There is another kind of darkening, which differs from that evident in *catenatus* and *horridus* in that an entire population is blackened instead of producing two pattern phases, a normal and melanistic, within the same area. This type of darkening may be more accentuated in some areas than in others occupied by the same

subspecies. The best example is the Arizona black rattlesnake (*C. v. cerberus*), which is quite dark, as the name implies. The darker specimens are from the higher elevations, the blackest being those from the Santa Catalina Mountains near Tucson. However, even these have small groups of yellowish scales along the dorsum, representing the interspaces between blotches. Young specimens are quite brightly marked. In all the snakes of this subspecies, the blotches become much more evident after preservation, for they turn dark brown, especially at their centers. In California and Baja California, in some mountain areas, the large adult Pacific rattlers (*C. v. oreganus* and *C. v. helleri*) are often quite dark, although the blotches are more apparent than in the darkest Arizona specimens of *cerberus*.

Hellmich (1951, p. 363) mentions three types of melanism in terms of color application, as originally suggested by Reinig: First, true melanism, in which the specimen is completely black; second, a change in the elements of the pattern by a broadening of the black markings (*nigrismus*); and, third, an increase in the number of black spots or dots (*abundismus*). The applicability of these definitions to the types of melanos or partial melanos occurring among the rattlesnakes will require further study, but it is believed that the third type, the abundance of the melanophores, produces the ecotypic effects in *oreganus*, *helleri*, and *cerberus*.

#### OTHER COLOR AND PATTERN ABERRATIONS

All species of rattlesnakes are subject to considerable degrees of variation in color and pattern. These variations may be individual, ontogenetic, or regional. In addition to these expected diversities, it is not uncommon to find individuals differing from their fellows to an extent verging on the freakish—that is, not constituting a regular or consistent proportion of the population. These divergences may be evident in color, pattern, or both. It is difficult to distinguish the genotypic from the phenotypic effects in this complexity.

Of the color aberrants, the most conspicuous are albinos and melanos, with which I have already dealt. But, as a matter of fact, there are many kinds of both a pale coloration—among which albinism is an extreme genetic deviation—and melanism, so that both partially white (or pink) as well as partly black specimens are not especially rare. Many of the aberrants seem to lack some particular element of the normal coloration, a sort of partial albinism. This may have the effect of bringing out some color hitherto masked behind, or within, a darker color, with which it may normally merge to produce an intermediate hue. It is particularly to be noted that a curtailment of the black pigment, melanin, may serve to stress hitherto unsuspected yellows and reds, especially the former. For example, Amaral (1932, p. 151) has described a case of xanthism in the South American rattler (*C. d. terrificus*). I have seen a number of instances of the same character in prairie rattlesnakes (*C. v. viridis*) from Kansas, South Dakota, and Colorado; various amounts of yellow or orange were apparent in the dorsal pattern, but no darker colors. Such specimens usually have pink tongues, whereas the anterior parts of the tongue are normally black in this subspecies. Gloyd (1935, p. 663) has described several specimens having this type of color deficiency. Yellow and red fade upon preservation of a specimen in alcohol or formalin, so that only live specimens give an accurate idea of the quality of this type of color anomaly.

Some aberrants, although still retaining, at least to a degree, the colors that nor-

mally comprise the pattern of blotches or rings, exhibit blotches so reduced in size that they approach obsolescence. This gives the snake a unicolored or mottled appearance. I have in my collection a specimen of the San Lucan diamond rattler (*C. r. lucasensis*) of this nature; it is an adult male. Although lighter than usual, this specimen does not lack melanin, which is evident in its black tail rings. I have seen mottled specimens of the prairie rattlesnake (*C. v. viridis*) exhibiting the same deviation from the normal pattern.

In snakes usually having blotches or rings, some aberration in the genic mechanism may cause a peculiar 90-degree rotation of the pattern, whereby transverse blotches or rings are transformed into longitudinal stripes. Probably the best-authenticated instance of this rotation is to be observed in the California king snakes (*Lampropeltis getulus californiae*); this has been discussed by the writer in some detail (Klauber, 1936d; 1939c). In one section of the territory occupied by this snake a considerable part of the population (some 40 per cent) comprises longitudinally striped specimens; the others have rings, which are normal in this species. As the distance from this central area increases, the aberrants become more infrequent and with less perfect longitudinal stripes, until territories are reached where only the ringed form occurs.

In aberrants of this type, the character of the longitudinal stripes that replace the rings or blotches depends on the nature of the detailed design of the normal rings or blotches. In the king snakes, the contrast between the light and dark rings constituting the usual pattern is very great and the boundaries are even-edged; and this effect is repeated in the sharp definition of the longitudinal stripes. But, in contrast, when a similar transformation occurs in indefinitely marked species, the change is less striking. For example, the gopher snakes (*Pituophis c. catenifer*) of central California sometimes have longitudinal stripes instead of the usual blotches; but, when they do, the stripes are not conspicuous, for they are neither sharply contrasted with the background in color, nor have they well-defined edges.

The same kind of pattern transformation has been observed among the rattlesnakes, but, as most of them are blotched, the longitudinal aberrants are not so conspicuous as are those among the king snakes. Furthermore, there are different degrees of transformation; in the rattlesnakes most of the aberrant specimens with longitudinal stripes are abnormal only anteriorly, usually for a fourth or less of the total length. Rarely, however, the entire pattern may be striped. It should be observed that the transformation does not merely consist of a coalescence of adjacent blotches, for each element of a normal blotch is represented in the stripe, particularly the dark inner edge and the lighter boundary. If the blotch ordinarily has a light center, this will be represented by a light vertebral line in the longitudinal stripe. Any secondary lateral blotches are usually manifested as longitudinal dark streaks below the main stripe. They may be broken into a series of dashes.

I have seen or heard of only three rattler specimens in which the blotch transformation into a stripe was complete. The first was called to my attention by M. Graham Netting of the Carnegie Museum, Pittsburgh. This was a timber rattler (*C. h. horridus*) from Franklin County, Pennsylvania, which has been described and illustrated by Gloyd (1935, p. 666, plate 103, fig. 2). As this is a species that normally has clearly evident crossbands, the longitudinal stripe is very definite and evenly outlined for a rattlesnake.

Another specimen, a western diamond (*C. atrox*) from Comal County, Texas, has a complete longitudinal stripe, but as this is normally a species with poorly outlined blotches, the stripe is not particularly clear. The central stripe is brown like the center of an *atrox* blotch. The darkest color is about five scale rows wide, but instead of a definite lateral border there is a gradual lightening, caused by both a lighter ground color and a reduction in the number and size of the dark-brown speckles that characterize this species. The tail is particularly interesting, for here the transformation is not only evident, but is striking. *C. atrox* is a species that has a tail quite different in pattern and color from the rest of the body, with the tan body color changing suddenly to a series of black rings on a gray background. As might be expected theoretically, in the aberrant specimen the black cross-rings are converted into a single black vertebral stripe, below which the sides are gray. Thus we have in this aberrant a complete pattern rotation from head to tail tip. The third specimen, also a western diamond, was for a time in the collection of the Witte Museum, San Antonio, Texas. It exhibits the same pattern anomaly as the one just described.

Specimens with anterior stripes are not at all uncommon, the extent of the stripe varying in length from the equivalent of two or three conjoined blotches up to one-half of the body or more. Of course, this indication of aberrancy refers to species normally blotched; the Neotropical rattler (*C. durissus*) and its relatives are characterized by a pattern of paired longitudinal stripes anteriorly, followed by blotches. The stripes usually extend from one to four head-lengths behind the head. Thus what is an aberration in most species has become the normal pattern in this one. Occasionally, in this species, the vertebral stripes are carried much farther back along the body than is normal. Amaral (1932, p. 82, fig. 3) shows a specimen of the South American rattlesnake (*C. d. terrificus*) on which the vertebral stripe extends for more than two-thirds of the body.

As I have said, partial striping is not a particularly rare anomaly among the rattlesnakes. I have seen anterior longitudinal stripes in the following subspecies: the Mojave rattlesnake (*C. s. scutulatus*), the Tamaulipan rock rattlesnake (*C. l. morulus*), the Queretaran dusky rattlesnake (*C. t. aquilus*), the red diamond (*C. r. ruber*), the prairie rattlesnake (*C. v. viridis*), the northern Pacific rattlesnake (*C. v. oreganus*), the southern Pacific (*C. v. helleri*), and the Panamint rattler (*C. m. stephensi*). Such freaks are particularly prevalent among the Mojave rattlers. One red diamond had a posterior, rather than an anterior, longitudinal stripe. A northern Pacific from British Columbia had a stripe in the mid-section. In a brood of 12 northern Pacifics from Arbuckle, Colusa County, California, all had aberrant patterns, in the form either of stripes on the neck or of series of greatly elongated blotches, some of which were split by light median lines.

Another form of anomalous pattern is produced by asymmetrical spacing in the blotch halves or the two sides of the middorsal line, this in species that normally have a single middorsal series. The blotches are connected by diagonal bars, each of which joins the posterior end of one blotch to the anterior end of the next blotch on the opposite side of the body. The result is a wavy, longitudinal stripe. I have seen this effect in specimens of *C. r. ruber* and *C. t. triseriatus*.

Another anomaly in pattern is the extension of the blotches down the sides to the ventrum. It is characteristic of many rattlesnakes that the anterior blotches

have well-defined lateral borders that separate the main blotch series—usually diamonds or hexagons—from the secondary blotches on the sides. Posteriorly, however, there is a tendency of the main dorsal series to coalesce with the side blotches, thus producing cross-bands. But with the exception of the ringed species *horridus* and *lepidus*, only the northern black-tailed rattler (*C. m. molossus*) has the anterior diamonds normally opened laterally so that the dark dorsal blotches extend down the sides. Occasionally an aberrant with this characteristic appears in other species. I have seen a perfect example of this in a red diamond rattlesnake (*C. r. ruber*) from northern Baja California; and Amaral (1932, p. 82, fig. 4) has called attention to the same deviation from normal in a South American rattlesnake from the state of Minas Geraes, Brazil.

In judging the accuracy or importance of reports of queerly colored rattlesnakes, one must have some knowledge of the species that are to be found in any area. For example, although most of the rattlers in the Wickenburg-Prescott section of Arizona are black, green, or brown, the report of an occasional bright-pink individual should cause no surprise, for the southwestern speckled rattlesnake (*C. m. pyrrhus*), one of the less-common kinds found there, is normally a beautiful coral pink in color. On the other hand, a newspaper report of a golden-yellow rattler seen near Porterville, California, may have had reference to a partial albino, for only one species of rattlesnake—the northern Pacific (*C. v. oreganus*)—occurs in that vicinity, and it is ordinarily gray, blotched with dark brown or black.

#### HYBRIDS

There are various myths concerning the hybridization of rattlesnakes with other snakes. Throughout the West, but particularly prevalent in the upper Missouri Valley, there is a widespread idea that the rattlesnakes have crossed with the bull snakes (*Pituophis*), producing an especially vicious and venomous offspring; which further, being rattleless, is the more dangerous since it does not warn its victims. There is not the slightest reason for believing this story; it probably gained credence from the fact that a bull snake on the defensive will vibrate its tail, and will coil and strike at an intruder. Those unfamiliar with the habits of snakes jump to the conclusion that such rattlesnake-like actions could only have been inherited from a rattlesnake parent. Actually, many kinds of harmless snakes will coil and strike, and quiver their tails when annoyed. However, involving no venom, the bite is innocuous; and the tail vibration is without sound, unless, perchance, it occurs among dry leaves, in which case a fair imitation of a rattle results. Another myth, heard in the Southeast, credits the copperhead with being the female of the diamondback rattlesnake. This is mentioned by Milling (1937, p. 43) as possibly having an Indian origin. The belief is related to the pilot-snake folklore that I have mentioned elsewhere (p. 1275).

But hybridization between rattlesnakes of different species does occur. Three specimens have been collected in the wild, which, because of the intermediacy of their characters, give every evidence of being hybrids between two species known to occur in the areas where the anomalous individuals were found; and at the San Diego Zoo we have had two instances of interspecies matings resulting in live young. Another occurred at the University of California, Berkeley.

First, with regard to the specimens found in the wild: Obviously it is impossible

to prove that these specimens were hybrids since nothing can ever be learned of their parentage. But, as they deviate strikingly from the normal individuals of the species found in the same neighborhood, and particularly because they are intermediate in pattern and squamation, the natural inference is that they are hybrids. This inference has been strengthened, now that hybrids of known parentage have been bred in captivity. In the case of wild anomalous specimens, the alternative theory that they belong to a previously undiscovered species must be considered, but this may be viewed as highly doubtful with respect to so conspicuous a creature as a rattlesnake, in any settled area where the fauna is well known.

In 1942 (p. 376) Dr. Reeve M. Bailey described what is apparently an intergeneric hybrid, that is, a cross between the two rattlesnake genera *Sistrurus* and *Crotalus*. The subspecies involved are the eastern massasauga (*S. c. catenatus*) and the timber rattler (*C. h. horridus*), both of which occur in the vicinity of Keokuk, Lee County, Iowa, where the supposed hybrid was found. No other kind of rattler inhabits that part of Iowa.

Dr. Bailey made a thorough tabular analysis of the characters of the hybrid, a female, compared with the known variations in the two possible parent stocks, and showed it to be intermediate in many characters. In others, it favored one parent race or the other, but without a convincing trend toward either. Through the courtesy of Dr. Bailey, I had the opportunity of examining this hybrid and determining certain body proportions—head to length of body; proximal rattle width to body length; fang length to head length—which I was then engaged in studying, and found the specimen intermediate in two proportions, while favoring *horridus* in the head-body ratio. Of all the characters investigated, the number of ventral plates was the most significant. This is an important and stable character. The hybrid was found to have more ventrals (163) than the highest known (157) among several hundred normal *catenatus*, and it had one less than the known range of *horridus*. Dr. Bailey reached the conclusion that the specimen must be a hybrid, and in this I concur. I tried considering it first as a possibly anomalous *catenatus* and then as an anomalous *horridus*. On either premise, the differences shown by this specimen, from the normal of the species to which it was tentatively assigned, were so many and extensive that one was impelled to the conclusion that it could not be a mere freakish offshoot of that species.

As to the second wild hybrid: I received in 1947 through the courtesy of Ross Allen a queer rattlesnake from Eufaula, Barbour County, Alabama. This is within the range of both the eastern diamondback (*C. adamanteus*) and the canebrake rattler (*C. h. atricaudatus*), and the peculiar snake has every appearance of being a hybrid between the two. The pattern is strikingly different from normal specimens of either form—sufficiently so to be immediately apparent to anyone familiar with the rattlesnakes of this area, which is why Mr. Allen sent it to me. The specimen is a young female 864 mm. (2 ft. 10 in.) long, with a complete string of four rattles.

The head marks are nearer those of *atricaudatus* than of *adamanteus*. The vertical light line on the prenasal and first supralabial scales, so characteristic of the latter species, is not present. Both species have a dark bar passing backward toward the angle of the mouth; in *adamanteus* this is edged above and below with sharply contrasting light lines, whereas, in *atricaudatus*, there is merely a bordering

light ground-color. In the hybrid these light stripes are intermediate, somewhat more apparent than in the canebrake, but less so than in the diamondback. The other head marks are more like those of *atricaudatus*.

The body blotches, although more irregular than is typical of the *adamanteus* diamonds, nevertheless have the brown centers, black edges, and light row of bordering scales characteristic of that species. There is no reddish vertebral streak such as is characteristic of *atricaudatus*; yet the blotches are like those of that species in shape, and in the fact that several of the anterior blotches are continued down the sides to engage the lateral secondaries. The ventral surface is intermediate in character between the two species, less mottled than in *adamanteus*, yet more so than is normal in *atricaudatus*. The tail rings are also intermediate, for they are more apparent than in *atricaudatus*, which, as its name implies, usually has a uniformly black tail, whereas *adamanteus* has clearly evident cross-rings of alternating black and gray.

In scale counts and arrangements, the two species have many similarities, so that these features of the supposed hybrid afford few indications of relationship. However, there is one important difference between them, this being in scale rows. Out of 72 specimens of *atricaudatus*, none has more than 25 scale rows at mid-body, whereas *adamanteus* usually has 27 or 29 (rarely 25 or 31). The hybrid has 29, thus strongly favoring *adamanteus*. The infralabials (18-18) are also high for *atricaudatus*, although in rare cases a specimen attains that many, but 18 is entirely normal for *adamanteus*.

In body proportions, also, the hybrid favors *adamanteus*. This species has a slightly larger head than the canebrake. Calculations, using the equations I have set forth in table 4:2, indicate that a snake of the size of the hybrid would, if an *adamanteus*, have a head about 45.3 mm. long, and if an *atricaudatus*, 37.5 mm. The head of the hybrid measures 42.8 mm. For snakes with equal head sizes, *adamanteus* has a relatively longer fang than *atricaudatus* (Klauber, 1939b, p. 45); in this, also, the specimen under examination is like the diamondback. The specimen is quite long for a four-rattle *atricaudatus* but is about normal for an *adamanteus*. The rattles, also, are larger than is normal for *atricaudatus*; in fact, each of the four rings is larger than the correspondingly numbered ring in any *atricaudatus* string I have measured, but all fall well within the range of dimensions of *adamanteus* rattles.

Summing up all these points, I should say that this specimen resembles *atricaudatus* somewhat more than *adamanteus* in pattern, but the reverse is true in squamation and form. It deviates from the normal of either species to such an extent that it either represents a previously undiscovered species—an untenable theory, having in mind the populous area in which it was found—or it is an *atricaudatus-adamanteus* hybrid, and I am convinced that the latter is the case.

The third wild hybrid that has come to my attention is a *ruber* × *helleri* cross from Rincon, San Diego County, California. Both the parent subspecies are common in that vicinity. It was brought to the San Diego Zoo on April 29, 1954, at which time it was about seven months old. It feeds readily and is thriving. Scale counts have not yet been made, but its intermediate pattern and color, particularly evident in the head marks, body blotches, and tail rings, leave no doubt as to its hybrid character. Besides, we have had available for comparison a captive-bred

brood (shortly to be described) having the same parentage, and thus are sure of its hybrid nature. However, in this instance we do not know which parent belonged to which subspecies. This is the first hybrid rattlesnake that has been recognized as such out of about 4,000 rattlers from San Diego County brought to the San Diego Zoo alive during the past 30 years.

The second kind of hybridization is that produced by the artificial associations of captivity. The first case of this type between rattlesnakes at the San Diego Zoo involved a male southern Pacific (*C. v. helleri*) and a female red diamond (*C. r. ruber*). The male was captured near the eastern border of San Diego City on March 9, 1937. The female was from western San Diego County, the exact locality being unrecorded; it was brought in as a young-of-the-year, having three rattles, in the summer of 1936. Both rattlesnakes were placed in a cage with some gopher snakes (*Pituophis*), to show the public that rattlers are not inherently vicious and live peaceably with other kinds of snakes. There were no other male rattlers in this cage, nor was the female ever in a cage with a red diamond male.

The Pacific male was observed courting the red diamond female in the spring of 1941, and mating was observed on February 2, 1942. Nine young were born on August 11, 1942. They seemed normal in every way, although one was about 10 per cent shorter than its fellows; however, such runts are by no means unusual in rattler broods. Five of the young snakes were preserved about two weeks after birth. It was hoped to raise the other four; however, one escaped from its cage shortly thereafter and was not seen again. By the following spring, only one of three that remained had fed, although food had been repeatedly offered to all, and the other two were preserved on February 27, 1943. It is not thought that their refusal to take food was in any way the result of their mixed parentage, for it is often difficult to get young rattlers to feed in captivity. At the time these two were preserved, they had grown hardly at all since birth, but the one that had accepted food, a male, had far outstripped them in size. This specimen became a vigorous adult (fig. 4:5), and lived until December 24, 1951, thus attaining an age of over nine years. We were never able to demonstrate its fertility, although it was given the opportunity to mate with individuals of several other species, including those represented by its parents, *helleri* and *ruber*. There may have been something amiss with its sense of sex recognition, as it courted males and attempted to dance with females—normally a strictly male-with-male activity.

Of the eight hybrids out of nine that were eventually preserved, there were four males and four females. Superficially those preserved as juveniles were much like the young of *helleri* at the same age, thus strongly resembling the father; they were considerably darker than any *ruber* of this size. The supraocular cross-dashes so characteristic of young *helleri* were present in some but absent in others; and the light stripe from the eye to the angle of the mouth was thinner than in *helleri*. The posterior half of the tail was bright yellow as in *helleri*, but superimposed, at least to a slight extent in all specimens and strongly in some, were the dark rings of *ruber*. The two juveniles that were longest retained alive had begun to develop a reddish tinge within the diamonds. The one that lived to become an adult changed greatly from its juvenile color, and eventually differed from either parental type, for it became tan with olive-brown blotches. The tail had irregular black crossbands with punctated gray between. Except for the tail, this specimen

resembled, more than any other variety of rattler, the northern Pacifics (*C. v. oregonus*) inhabiting the arid west side of the San Joaquin Valley, or the Mojave rattler (*C. s. scutulatus*).

In scutellation, the hybrids fall between the parental forms. *C. v. helleri* and *ruber* do not differ in all categories, by any means, but, where they do, the hybrids are intermediate. *C. v. helleri* usually has 25 scale rows, but often has 27 and, rarely 23 or 29. *C. r. ruber* usually has 29, but often 27 or 31, and, very rarely, 25; the mother of the hybrids had 29. The hybrids have 25(3), 26(1), and 27(4). The ventral

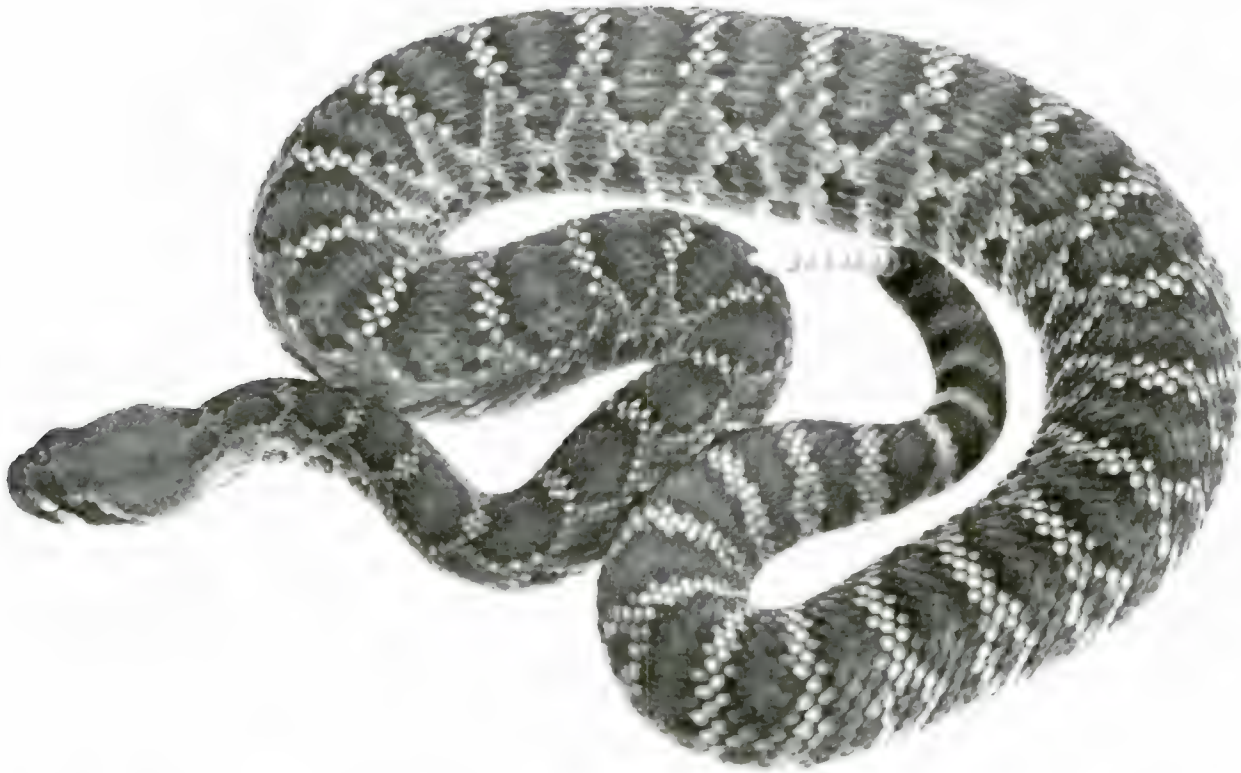


Fig. 4:5. Adult male hybrid rattlesnake. Father a southern Pacific rattlesnake (*C. v. helleri*); mother a red diamondback (*C. r. ruber*). This snake and its parents are shown in color in the frontispiece of volume II.

scales in the male hybrids (with one exception) number more than the highest ever recorded in male *helleri*, and close to or above the recorded limit in the case of the females. All except one are within the normal *ruber* range, but below the average. The caudals and the labials overlap in the two species so that the trends in the hybrids are in no way significant.

There is one scale characteristic more often found in *ruber* and its relatives than in any other rattler; and another peculiar to *helleri* and related subspecies. As to the first, somewhat over 90 per cent of the red diamonds have divided first infralabial scales, yet none of the hybrids had this peculiarity. Unfortunately, the mother also lacked it, which may partly explain its nonappearance among the offspring.

The southern Pacific peculiarity—in common with other subspecies of the western rattlesnake (*C. viridis*)—is the possession of more than 2 internasals. More than 90 per cent of specimens of *helleri* have more than 2 internasals, whereas *ruber* always has but 2 only. Among the hybrids three had 2, three 3, one 4, and one 5.

The father had 3. Thus, the hybrids exhibit a tendency to inherit this anomaly of the father's race, although the proportion with only 2 internasals ( $37\frac{1}{2}$  per cent) is much greater than is normal in *helleri*. In *ruber* there are usually prefoveals or postrostrals between the prenasals and the first supralabials; in *helleri* such scales are rarely present. In the hybrids they are present in 11 out of 16 counts, so the compromising effect of the mixed parentage is again evident.

The red diamond rattler is a somewhat larger rattlesnake than the southern Pacific. It is of interest to record that, except for the runt, the hybrids at birth were fully 10 per cent longer than is normal for the young of the *larger* subspecies. Red diamond and southern Pacific rattlesnakes occur together over large areas of southern and Baja California. Yet hybridization in the wild must be of very rare occurrence, since only one hybrid has been brought in to our local scientific institutions during the past 30 years.

The second instance of hybridization among rattlesnakes at the San Diego Zoo involved a male Mojave rattlesnake (*C. s. scutulatus*) from near Tucson, Arizona, and a female Aruba Island rattler (*C. unicolor*). The mating was an entirely accidental one, that is to say, the snakes had been put in a cage together only because separate cages were lacking. The mating was not actually seen, although the male had been observed courting the female on several occasions. There was another male in the cage at the time, a Great Basin rattler (*C. v. lutosus*), but it did no courting, and, besides, the resemblances of the young to the Mojave rattler leave no doubt as to their paternity. No male *unicolor* was present in the cage at the time breeding must have occurred, and, although one was introduced later, both the character of the young and the time element involved prevented this snake from having been considered the father. The mother was about a year old—she had a five-rattle complete string—when she arrived at the zoo in August of 1946. Four young were born June 10, 1948, at which time the mother had 10 rattles, and presumably was somewhat over two years old.

The two subspecies involved do not, of course, ever meet in the wild, since *C. unicolor* is found only on Aruba Island, off the coast of Venezuela, and *C. s. scutulatus* inhabits the southwestern United States and northern Mexico; however, two related forms, the Huamantlan rattlesnake (*C. scutulatus salvini*) and the Central American rattlesnake (*C. durissus durissus*) do occur together in Veracruz, where they might, but probably do not, hybridize.

The four  $F_1$  (first generation) members of this brood, now fully adult, are still alive at this writing (June 15, 1954) and therefore detailed morphological studies cannot be made. Superficially they look much like Mojave rattlesnakes, although the colors and markings are brighter and more clean-cut than is usual in that subspecies (fig. 4:6). They are tan instead of green, as are most specimens of *scutulatus*; however, tan or brownish specimens do occur in parts of Arizona. The paravertebral stripes on the head and neck typical of the *durissus* group are present only on the heads of three specimens, but do extend for about a head-length onto the neck of the fourth. (The father also had a neck stripe, an occasional aberrancy in *scutulatus*.) The light unmarked scales that border the dorsal blotches, as noted in normal *scutulatus*, are present. The tail rings are alternately black and punctated gray; in this they are a compromise between the sharply contrasting black and light-gray rings of *scutulatus*, and the almost patternless dark-gray tail of *unicolor*.

The first lobe of the rattle matrix is mottled, as in *scutulatus*. The patterns disappear in adult specimens of *unicolor* but no such tendency is evident in this brood at an age of six years.

*C. unicolor* is characterized by a vertebral ridge; although this is less conspicuous than in the mainland subspecies, *durissus* and *terrificus*, it nevertheless is more prominent in *unicolor* than in *scutulatus*. The hybrids possess this ridge to a minor degree. In the four hybrids, the button widths vary from 5.0 to 5.4 mm., with a mean of 5.2. This is larger than the buttons in *unicolor*, which average 3.4; in *scutulatus* the average is 5.7 mm., and thus the hybrids slightly favor the father.

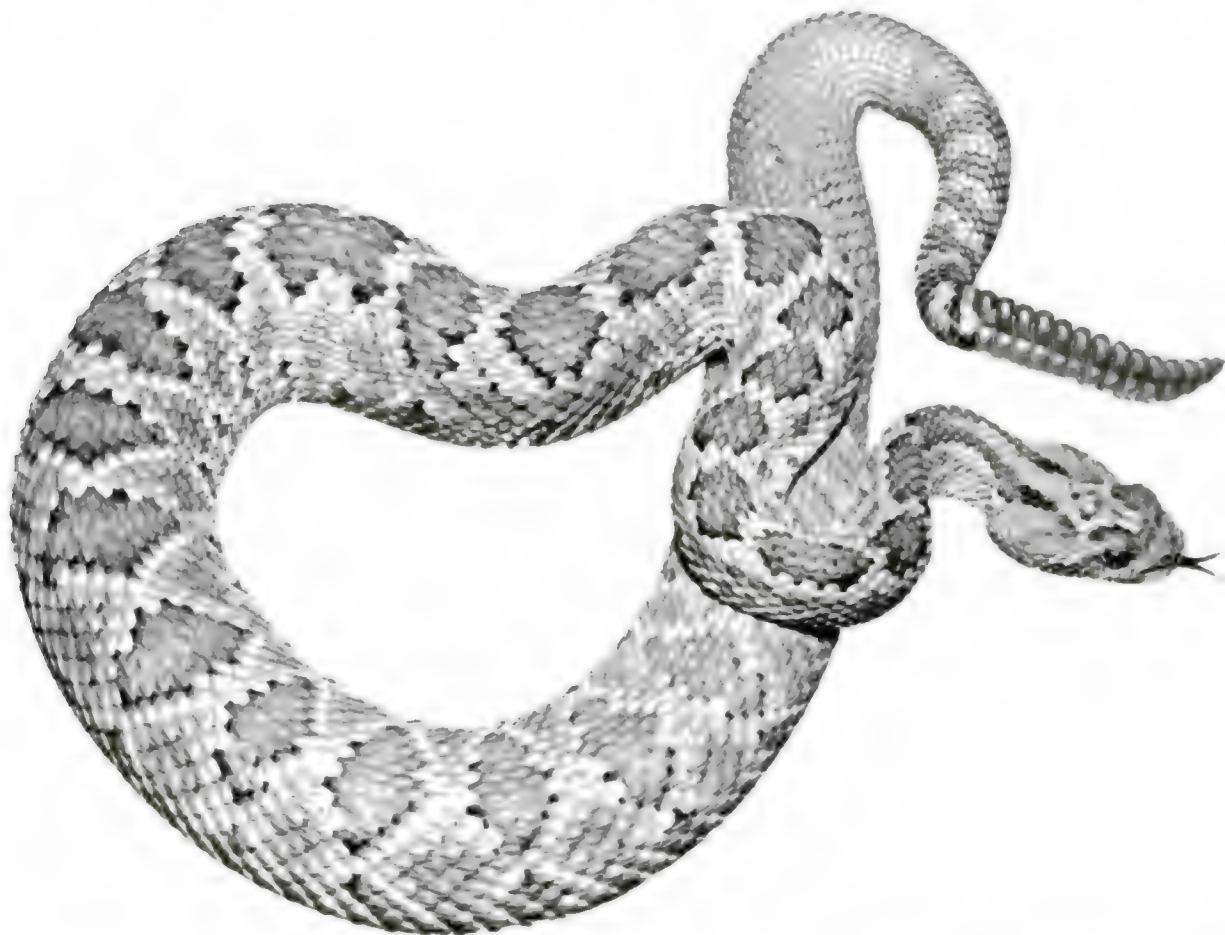


Fig. 4:6. Adult male hybrid rattlesnake. Father a Mojave rattlesnake (*C. s. scutulatus*); mother an Aruba Island rattlesnake (*C. unicolor*). (Photograph by G. E. Kirkpatrick.)

Since birth, these four  $F_1$  *scutulatus-unicolor* hybrids have been kept together, but isolated from other snakes, and the single female has given birth to no less than five  $F_2$  (second generation) broods. Whether the same male was responsible for all five broods is not known; it is probable that the first and third broods had the same father, as mating was observed. A second male was seen to be courting prior to the birth of the second brood. The statistics of the five broods are:

Brood number	Date of birth	Living young	Dead young	Defective eggs
1	4-28-51	5	1	1
2	3-20-52	5	-	-
3	1-20-53	10	3	1
4	7-21-53	8	1	1
5	6-18-54	6	-	-
Total		34	5	3

The average interval between broods was nine and a half months, and the minimum six months, a surprisingly short time. The gestation periods for the first and third broods were 170 and 187 days, respectively.

Lest the proportion of dead young and infertile eggs in these  $F_2$  broods be charged against hybridization, the following statistics of pure *unicolor* broods born to the mother of the  $F_1$  *scutulatus-unicolor* brood subsequent to the birth of that brood are given:

Brood number	Date of birth	Living young	Dead young	Defective eggs
1	6-27-51	1	2	6
2	6- 5-52	7	-	2
3	5-13-53	8	1	1
4	4- 5-54	7	-	-
		—	—	—
Total		23	3	9

It will be observed that the proportion of the defectives was no greater in the  $F_2$  hybrid broods than in the pure *unicolor* broods.

To date, the zoo has not been successful in bringing any of the  $F_2$  hybrids beyond the juvenile stage, despite efforts to get them to feed. Three of brood No. 3 did eat but still did not survive. As this is written, one of the fifth brood is still alive at an age of 1½ years. B. H. Brattstrom made an anatomical examination of the first  $F_2$  brood and found among the five born alive and apparently normal that three lacked a proper differentiation of the stomach from the rest of the digestive tract, besides which two of these had unusually small hearts, livers, and reproductive organs.

Since *scutulatus* and *unicolor* are not greatly dissimilar in many characters, to see whether the hybrids are intermediate it is necessary to investigate those characters showing the widest divergence. These are the ventrals, the scales anterior to the supraoculars, certain other head scales, and the body blotches. *C. unicolor* is lower than *scutulatus* in ventrals, but there is virtually no gap between the maximum *unicolor* counts and the lowest *scutulatus*. The  $F_2$  hybrids all fall within the *scutulatus* range, although well below the average for that species.

The best evidence of the intermediate character of the hybrids is furnished by the scales in the internasal-prefrontal area of the crown. In 35 out of 36 specimens of *unicolor* these scales (not counting supraloreals) numbered 4; the other had 6. In *scutulatus* they range from 6 to 20, or more, with an average of about 12. Specimens with fewer than 8 are exceedingly rare; only 3 out of 479 had as few as 6. In the  $F_1$  hybrids, these scales numbered 4(1), 5(1), and 6(2); in the  $F_2$  hybrids 4(11), 5(3), 6(6), 7(6), 8(5), 9(2), 11(1), 13(1), mean 6.5. It will be observed that the counts have an intermediate tendency, but that the dispersion increases, and this toward *scutulatus*, in the  $F_2$  broods. The same trend is observable in certain other head scales, for divided first infralabials, intergenials, and submentals are of frequent occurrence in *unicolor* but rare in *scutulatus*. In the hybrids they are present with an intermediate frequency.

The body blotches, which are fewer in *unicolor* than in *scutulatus*, tend also in the hybrids to fall low in the *scutulatus* range. The statistics are: *unicolor* 18 to 28, mean 23.2; *scutulatus* 27 to 44, mean 36.6; hybrids 26 to 38, mean 32.9. The

hybrids' blotches are much more irregular in color, size, and shape than is normal in either parent species. Paravertebral stripes are evident on the neck in most specimens, but they are shorter than is usual in *unicolor*; they are not normal in *scutulatus*, although they were present in the father of the  $F_1$  brood. Two  $F_2$  specimens have long mid-body streaks. The tail rings also are intermediate, for they are more evident and darker than in *unicolor*, but less sharply outlined than in *scutulatus*.

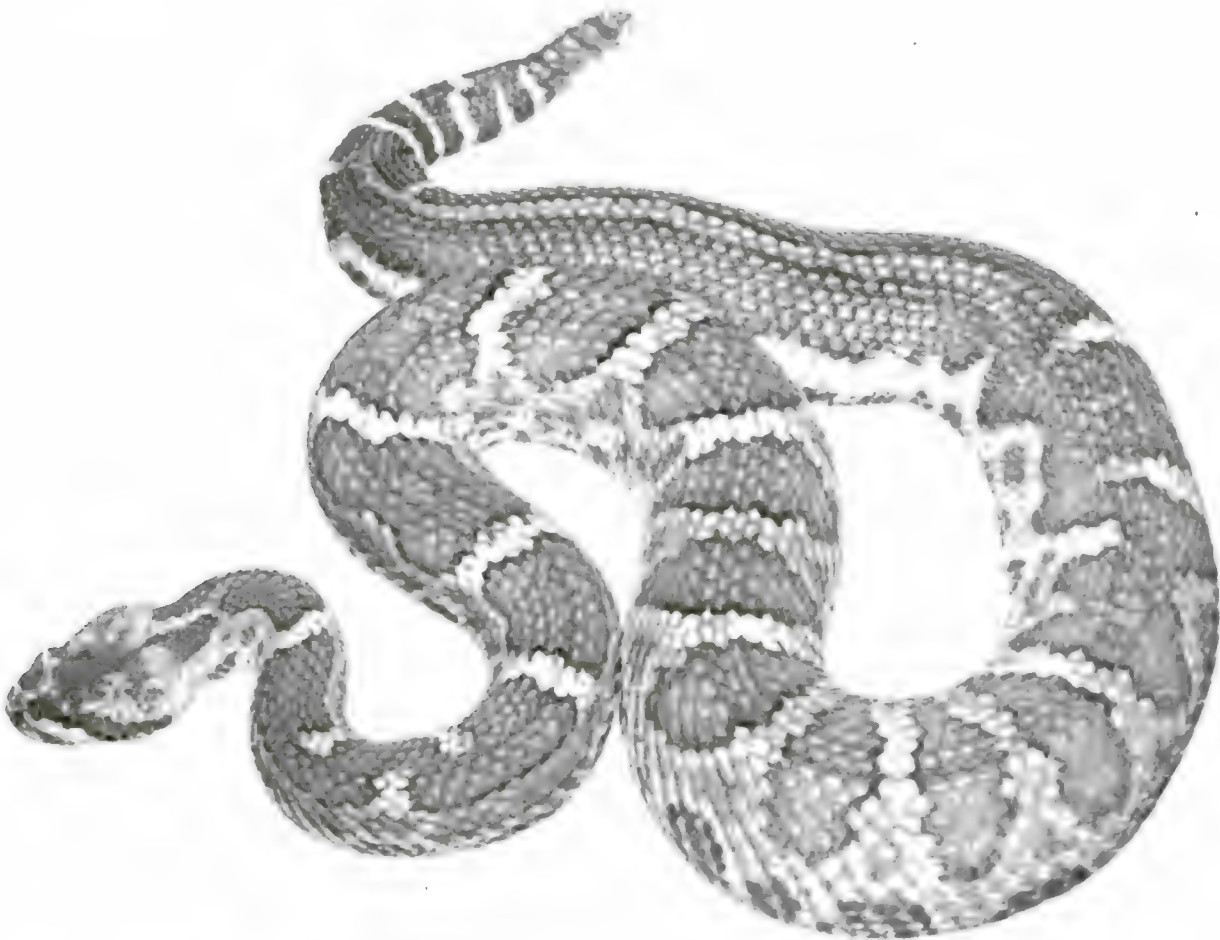


Fig. 4:7. Adult female hybrid rattlesnake. Father a northern Pacific rattlesnake (*C. v. oreganus*); mother a Mojave rattlesnake (*C. s. scutulatus*). (Bred in captivity by Sherburne F. Cook, Jr. Photograph by G. E. Kirkpatrick.)

It is of particular interest to note the intermediacy of these hybrids with respect to meristic characters, for many animals in which hybridization has been studied do not have countable characters.

Sherburne F. Cook, Jr., of the University of California, Berkeley, had a brood of hybrids resulting from the mating of a male northern Pacific (*C. v. oreganus*) from Mt. Diablo, Contra Costa County, California, with a female Mojave (*C. s. scutulatus*) captured one mile north of Mojave, Kern County, California. The snakes mated in May of 1952 and 12 young were born in October. Two of the young died within a few months after birth and were not preserved. Of the rest, three are still alive at the San Diego Zoo at the age of three years; the remaining seven have been preserved, and are now in my collection through the courtesy of Mr. Cook.

The parent subspecies, whose ranges may overlap in the southeasterly fringes of the Tehachapi Mountains in Kern County, California, do not differ in the more important scale series such as dorsal scale rows, ventrals, and labials. Their most important differences lie in the scales on the top of the head, for the *scutulatus* scales on the crown are less subdivided than those of *oreganus*. The following statistics show the degree to which the hybrids are intermediate: *C. s. scutulatus*, like most rattlesnakes, has two internasals; of *oreganus* only about 14 per cent have less than three. Among the hybrids the counts are: 2(6), 4(2), and 5(2). The scales occupying the internasal-prefrontal area in *scutulatus* range from 6 to 21, with an average of 11.5; in *oreganus* they range from 10 to 46, with an average of 24.3. In the hybrids the spread is from 13 to 25, with a mean of 18. Finally, there are the minimum intersupraoculars. In *scutulatus* these usually number 2, although there may be as many as 4. The mother was somewhat anomalous in that she had 3. In *oreganus* the range is from 2 to 9, most specimens having 4 (17 per cent), 5 (30 per cent), or 6 (33 per cent). The hybrid brood has this distribution: 3(4), 4(4), 5(1), 6(1). It is evident that, as was true of the other hybrids, in these meristic characters of squamation these hybrids are intermediate between the parent races.

In pattern the hybrids are unlike either parent. The dorsal blotches are unusually large, and four specimens have blotches that merge into longitudinal stripes, posteriorly in three, and both on the neck and near the tail in the other (fig. 4:7). As is characteristic of specimens of *C. v. oreganus* from northwestern California, as they age, the hybrids tend to lose the marks on the sides of the head below and forward of the postocular dark streaks, thus becoming white-faced. The body coloration, otherwise, is intermediate between *oreganus* and *scutulatus*.

Although no other cases of hybridization among rattlesnakes are known to me at present, I have no doubt that others, both in the wild and among captive specimens, will be in evidence from time to time. At the San Diego Zoo, rattlers of one species have often been observed courting those of others. Davis (1936, p. 268) has reported the mating, in captivity, of a male northern blacktail (*C. m. molossus*) with a female western diamond (*C. atrox*). Whether the union proved fertile is not known. W. E. Haast, of Kendall, Florida, informed me that he had observed *atrox* and *adamanteus* mating in captivity. No doubt, in time, experiments in artificial insemination will be successful.



## 5. The Rattle

### HISTORICAL

The rattle is the peculiar attribute of the group of New World snakes that form the subject of this study. This remarkable appendage, whose purpose has been a source of speculation and controversy ever since these snakes were first observed by European naturalists with an astonishment approaching incredulity, is a fruitful subject of research. For we have in this organ a mechanism that is unique in both development and function; and it is worth while not only to study it as a queer animal instrument, with its parts unchanged by growth and time, but to follow, also, the gradual emergence of accounts of the rattle from a plane of myth and folklore to one of understanding, although admittedly with problems still unsolved.

First, as to the development of European knowledge of the rattle and the origin of some of the peculiar beliefs as to its structure and use: The earliest reference to the rattle<sup>1</sup> in print, as far as I have been able to determine, was made by Magalhães de Gandavo in 1578 (fol. 24r; Stetson, 1922, vol. 2, p. 63). In this short account two important ideas were presented: First the myth—persistent for two hundred years or more thereafter—that the rattle sounds whenever the snake moves; and, second, that passersby, when they hear the rattle, avoid the snake. In this second statement there is a suggestion both of the accepted theory of the function of the rattle and of its origin and development.

The first mention of the rattle in English referred only to its use by the Indians as an ornament; this is contained in an account of Virginia by Captain John Smith (1612, p. 20).

The indestructible rattle-per-year myth was first stated in print by Hernández in 1615 (fol. 192r); he likewise observed (correctly) that the rattle was sounded furiously when a snake is angry or molested. Hernández' work subsequently went through two Latin editions (1628, p. 328; 1651, p. 328), and was plagiarized by Nieremberg (1635, p. 268), who is often given the credit for Hernández' discoveries. The rattle-per-year theory was also mentioned by Vázquez de Espinosa in 1629 (1948, p. 197), and, in 1648, by both Piso (p. 41) and Marcgravius (p. 240). Piso was the first to publish the belief that the rattle itself is a dangerous weapon—more deadly, in fact, than the snake's fangs and venom. This myth was current

<sup>1</sup> Cieça de Leon (1554, fol. 25) had mentioned the snake, but not the rattle.

for a time, but died out within a hundred years or so. Marcgravius was the first to describe the composition and color of the rattle. Jonstonus (1653, p. 26; 1657, p. 23), whose natural histories became deservedly popular, was the means of giving a more widespread circulation to the opinions of Hernández (via Nieremberg), Marcgravius, and Piso. He gave due credit to his sources.

Glover (1676, p. 631) was the first to attribute the warning effect of the rattle to Divine Providence. Grew (1681, p. 50) gave the first adequate description of the internal structure of the rattle. He clearly understood the multiplication of the sound produced by the clashing of the successive lobes against each other. He doubted that the rattles indicated accurately the age of the snake, and found no verification of Piso's theory that the rattle itself is a dangerous instrument, a belief denied by Tyson (1683, p. 53) as well. Tyson noted, correctly, that the flat side of the rattle is perpendicular to the ground, rather than parallel as shown by Nieremberg in a picture. This is often misunderstood, even to the present day.

Clayton (1693, p. 126) stated, quite erroneously, that young rattlers have no rattles for a year or so after birth. He was probably confused by the young of some other kind of snake, but, at any rate, this notion still persists. He likened the rattle substance to that of a horn or fingernail. Beverly (1722, pp. 64, 261) was one of the first, if not the first, to state that the rattle is invariably sounded as a warning before the snake strikes. Kalm (1752-53, p. 316) questioned this supposed altruism of the rattler, but this bit of folklore is still widely accepted.

Dudley (1723, p. 294) was the originator of the exaggerated rattle string, for he tells of the killing of a rattlesnake with 70 to 80 rattles, a yarn often recurring in subsequent accounts; he also (p. 293) was the first to report that the Indians were afraid to travel through the woods in wet weather, since the dampness rendered the warning rattle inaudible. He further stated that when one rattler sounded off, all those in the vicinity would take up the chorus; it had previously been reported by Neal (1720, p. 574) that the rattle was used by a snake as a call upon its fellows for assistance.

The early writers inferred a bell-like sound to the rattle, which probably few, if any, had ever actually heard as vibrated by a live snake. The English no doubt got the bell idea from the translation of the Spanish *cascabel*, and Portuguese *cascavel*, words for the rattle—as well as the snake—used by the early explorers. This characterization of the noise was related to the erroneous idea that the rattle is sounded automatically whenever the snake moves. The earliest appropriate description of the sound was that of Megapolensis (1644; 1909, p. 169), who likened it to that of a cricket. Since crickets, locusts, and cicadas were often confused in those days, it is possible that he had a cicada in mind, for the sound produced by some cicada species does strongly resemble that of a rattle. Budd (1685, p. 35) thought the sound similar to that of a child's rattle. Kalm (1752-53, p. 313) likened it to that of many spinning wheels heard at a distance, a much less appropriate simile.

Statements regarding the rattle that were made in the early days, but not published until many years later, did not, of course, affect contemporary thought; however, they are of interest in indicating what the opinions then current may have been. Soares de Sousa (1938, p. 308), writing in 1587 of the wonders of Brazil, presented these facts about the rattle: The noise made resembles that of

a bird lure; the rattle sounds whenever the snake moves, thus warning people away; the Indians believe the rattle itself to be very dangerous; the number of rattles indicates the age of the snake, for a new rattle is acquired each year. Since similar ideas were subsequently advanced by Hernández, Piso, and others who are not known to have had access to de Sousa's manuscript, we may assume that these beliefs were current among the natives, and were not European inventions, as were some of the notions regarding rattlers subsequently attributed to the natives.

To Hernández belongs the credit for the first published picture of a rattlesnake and its rattle (1628, p. 329). It shows a coiled rattler (fig. 17:1, this book), with the rattle pressed too close to the body for a clear view, although it is accurately drawn. Nieremberg (1635, p. 268), who plagiarized Hernández' work, improved the picture by showing the rattle somewhat separated from the body coil (fig. 17:2); however, the rattle is turned as if it were carried with the widest face parallel to the ground, instead of perpendicular as is actually the case. Nieremberg's figure was subsequently reprinted (with due credit) by Jonstonus (1653, plate 7; 1657, plate 7) and by Owen (1742, plate 6), and thus was given a wide circulation through these popular works.

The first independent picture after Hernández', was probably that of Piso (1648, p. 41), which shows a crawling, rather than a coiled rattler (fig. 17:3). Other early illustrations were published by Olearius (1674, plate 11), Grew (1681, plate 4), and Tyson (1683, figs. 10-12). Grew shows a three-lobed rattle separated from its string, and Tyson presents the first picture of the shaker. Catesby (1743, vol. 2, plate 41) was the first to show a cross section of a rattle (fig. 17:5).

This concludes a summary of the development of the European knowledge of the rattle. I have treated elsewhere (p. 1196) its use by the Indians in medicine and for ornamentation (p. 1207). In other chapters there will also be found the corresponding uses of rattles by whites; for medicinal uses see p. 1271, and for decorative uses p. 1059.

## FUNCTION AND UTILIZATION

### THE FUNCTION OF THE RATTLE

The literature and folklore of the rattle are replete with speculations upon its function; these have been proposed in great variety since the earliest encounters between man and rattlesnake. Even today, when there is a practically unanimous agreement, among those herpetologists who have had a wide field experience with rattlesnakes, that the rattle is a warning mechanism, the statement may still be seen that its function is in doubt (Arnold, 1935, p. 133; Ditmars, 1936, p. 337; Gillespie, 1937, p. 132; Curran and Kauffeld, 1937, p. 51; De Lys, 1948, p. 73; Devoe, 1951, p. 226). But, as one reviews the literature, one notes that most of the criticisms of the accepted warning theory have resulted from a failure to specify the circumstances under which the rattlesnake employs the warning, and the character of the creature warned. When these are defined, the usual criticisms of the warning theory are adequately answered. The problems that remain concern the evolution of so remarkable an instrument.

I shall first review some of the theories of the function of the rattle that have

been advanced. These may be divided into 4 broad categories, involving: (1) purposes other than the conveyance of sound; (2) sounds intended for other rattlesnakes; (3) sounds intended for prey; (4) sounds aimed at other creatures.

Before discussing these categories—and each is divisible into a number of sub-classes—I shall amplify one fact that has a bearing on the credibility of several of the theories, namely, the infrequency with which rattlers are heard to rattle while undisturbed in the wild. Certainly it has been the experience of those of us who live in areas where rattlesnakes are quite common, that we almost never hear one unless we ourselves have disturbed it. Chateaubriand (1828, vol. 2, p. 163) claimed that the love calls of the rattlers were the only sounds to strike the ear of the traveler at noon in the heat of the forest wilderness. I know of no one who has heard such a chorus, or has had an experience paralleling that of Roberts (1930, p. 185), who thought he had heard snakes rattling continuously all one night in British Columbia. I can only presume that the sounds came from other sources.

Returning to the discussion of theories of the purpose of the rattle, there is, in the first category—purposes other than the production of sound—only one that was ever taken seriously; this was Piso's claim (1648, p. 41) that the rattle itself is a poisonous instrument, more dangerous to man than the fangs and venom. This seems to have been a widely current Brazilian myth, since it was mentioned in 1587 by Soares de Sousa, whose description of Brazil was not actually published, even in part, until 1825, and was probably unknown to Piso in manuscript. Although this belief was given further publicity by Jonstonus' popular natural history (1653, p. 26; 1657, p. 23), it was denied as early as 1681 by Grew (p. 51) and by Tyson (1683, p. 53), and has received little serious consideration since.

An echo of this idea, in modern folklore, is the myth that rattle dust is poisonous (Anon., 1897, p. 135; Dresslar, 1907, p. 49). Indeed, Spaulding (1944, p. 151) records the myth that a snake rattles, not to make a sound, but to shake the poisonous dust into an intruder's eyes.

Garman (1889, p. 176) thought that tail vibration by snakes—a widely existing nervous reaction upon the part of a threatened or angered snake, which is by no means restricted to rattlers—might be designed to protect the tail from enemies, or to draw the attention of prey away from the threatening head. Since this ophidian custom of vibrating the tail was important in the genesis of the rattle itself, these hypotheses, if verified, would have a bearing on the function of the rattle. But I know of no facts supporting them.

The first of the functional theories involving the sound of the rattle assumes its purpose to be an exchange of signals between rattlesnakes, either (a) as a mating call, or (b) as a warning to, or call for help from, other rattlers.

The mating-call theory was popular during the middle of the last century, receiving support from Chateaubriand (1828, vol. 2, p. 163), Wuerttemberg (1835; 1938, p. 265), Putnam (1872, p. 693), Aughey (1873, p. 86), Coues and Yarrow (1878, p. 263), Hopley (1882, p. 312), Townsend (1882, p. 245), Ingersoll (1883a, p. 40; 1884a, p. 402), and Garman (1883, p. xxvi); and more recently from Babcock (1929b, p. 27), De Lys (1948, p. 73), and Moore (1951, p. 229). Aughey (1873, p. 85) told of watching a snake that was rattling intermittently. Shortly

another rattler made its appearance and mating ensued. This is the only instance of which I have knowledge, in which such an occurrence was claimed to have been witnessed, the other advocates of the mating theory either basing their opinions on supposed logic, or on Aughey's tale. Koenig (1906, p. 49) assumed that male and female rattlers made different sounds with their rattles, but said the difference had not been determined.

Against the mating theory various arguments may be advanced. Moran (1878, p. 262) has pointed out how rarely the sound of the rattle is heard in the wild, which fact I have mentioned previously. Rattlesnakes are common in the chaparral and desert areas of southern California. From observations of mating pairs found afield, the mating season—about 4 weeks in the spring—is well defined. It is inconceivable that, if the rattle were a mating call, it would not be frequently heard during this climactic period of rattlesnake activity; yet it is not. The courting pattern of male rattlesnakes is known from observations of large numbers of attempted and successful matings of captive snakes. The pattern is basically uniform, that is, much the same among the many different kinds of rattlers, yet in no case has the use of the rattle been noted. Of course, if a rattler intent on mating is disturbed, then the rattle is used, but only as a warning to the intruder. Mitchell (1903, p. 36) stated that the males are especially aggressive and will the more promptly rattle at a disturber during the mating season. This might be confused by an inexperienced observer with the use of the rattle as a sex call.

No advocate of the mating theory can claim that the mating call is the sole use of the rattle, for, as is well known, immature snakes, when disturbed, sound the rattle as readily as adults, and females as readily as males; indeed, the freshly born infant just out of its fetal sheath will vibrate its soundless button and threaten an intruder with all the spirit of its elders. Surely this instinctive reaction can have no relation to the sexual instinct. Garman (1883, p. xxvi), in advocating the sex-call theory, claimed that the rattle of the courting snake was used with less stridency than when sounded in anger. Wuertemberg (1835, p. 265) suggested the use of an artificial rattle to decoy romantic rattlers to their destruction, a suggestion heard repeated in San Diego County within the last few years. But we must conclude that the extended observations of recent years lend no support to the mating-call theory.

The exchange of signals between rattlers for mutual warning, protection, or attack, has been suggested by a number of authors. It stems from the observation—which has a factual basis—that when a group of rattlesnakes is gathered together and one rattles, several or all may join the chorus (Dudley, 1723, p. 293; Wesley, 1784, ed. 4, vol. 2, p. 37; Hopley, 1882, p. 312; Rutledge, 1931, p. 646; 1935, p. 525). A. M. Jackley had this to say on this point: "When one rattles, those nearby, whether concealed or in sight, become alarmed. Whether they sense the vibration from the air or the ground, I don't know."

This suggestion of mutual alarm led to the related theory of mutual assistance. Neal, as early as 1721 (vol. 2, p. 574), had presumed that the rattle served as a call to arms, and this was repeated by Oldmixon (1741, vol. 1, p. 187) and Gillam (1916, p. 132).<sup>2</sup> Aughey (1873, p. 86) tells of a rattler attacked by hogs; it rattled

<sup>2</sup>The tall-story addicts eventually carried this call-to-arms propensity to its logical conclusion. In eastern Kansas, so they say, the tocsin is flashed from one den to the next, and soon all the 200 million rattlers in that section of the state are rattling in unison, and the human inhabitants quickly flee to their cyclone cellars (Davidson, 1913, p. 188; Davidson and Blake, 1947, p. 270).

for assistance and three others came at once, to their own destruction. A similar story is told by Chalmers (1878, p. 422); and Ingersoll (1884a, p. 403) states that such a response to a call for help was observed among captive rattlers. Kunzé (1879, p. 333) thought that a captive snake rattled more frequently as the time of hibernation approached, and therefore presumed the sound to be an assembly call.

Observations of a great many captive rattlers, as well as field experiences, lead me to place no credence whatever in this theory of mutual-aid pacts. True, alarming one rattler of a group may cause others to rattle, but usually this can be attributed to the same disturbance—a visible movement of the intruder, or his foot-fall—that caused the first snake to be aroused, without any necessity for the assumption that the alarm was communicated by the rattle. Indeed, when the first snake sounds its rattle it almost always rises into the striking coil, and this movement may well alarm its fellows. The hoofbeats of hogs attacking one rattler would certainly alarm others within a considerable radius, which explains the Aughey-Chalmers stories.

On several occasions in the field, I have come upon two or three rattlers together. One, alarmed at the intruder, would rear up and rattle violently, yet the others a few feet distant often remained quite unperturbed. C. B. Perkins has observed that a rattler in captivity will sometimes rattle when a second snake approaches food that the first has struck or is eating. This is a rather natural extension of the use of the rattle as a warning; it is like the growl of a dog, and shows that rattlers do not change this primary purpose of the rattle when using it on their fellows.

Finally, as a conclusive argument against either the mating-call or call-for-help theories, the fact should be cited that rattlers are quite deaf to the sound of the rattle. Elsewhere (p. 391) I have discussed the hearing ability of rattlesnakes; and how an extraordinary sensitivity to vibrations of the substratum upon which a snake rests, would lead one to suppose that rattlesnakes can hear, whereas they are, in fact, quite deaf. Such experiments as I have conducted, which are detailed elsewhere, confirm the belief originally expressed by Manning (1923, p. 247), that no rattler ever heard another's rattle.

A number of theories regarding the purpose of the rattle have to do with its effect on the snake's prey. Concepts within this category suggest the following methods of use:

- To charm the prey with sweet sounds
- To attract the attention of prey, and thus to bring it within the influence of the snake's power of fascination—its baleful glance
- To paralyze the prey with fright, or to startle it into immobility
- To decoy the prey through curiosity
- To lure the prey by an imitation of the cicada or some other insect, or by an imitation of running water
- To warn the prey to escape

The many writers of the past who have advocated the prey theories have not always made the sharp distinctions that I have indicated in this list; often they have been couched in such generalities as: "The rattle is a means of securing prey." But I think a survey of the possible validity of the suggestions will be clarified if we indicate, in each case, the rattle's presumed method of operation.

Some authors have suggested the use of the rattle as a warning to prey. Others have seized upon the obvious fallacy of such a theory—predators never warn their victims—as a refutation of the entire warning theory. I shall return to this peculiar semantic aberration in due course.

In considering all theories suggesting that the rattle is a prey-securing mechanism, it is necessary to mention again the infrequency with which undisturbed rattlers—I mean undisturbed by the observer himself—are heard rattling in the field. Surely, in the spring in snake-infested areas, the hungry snakes would be heard everywhere broadcasting their lures or charms, and rattler-collecting would be appropriately expedited. No such condition exists. As early as 1752, Kalm (p. 317) was told by the Indians that the snakes never rattled when lying in wait for food, and time has confirmed the accuracy of this observation.

Some of the theories of the charming or fascinating of prey by rattlesnakes involve the use of the rattle as a part of the procedure. The advocates of these theories believe it effective in one of three ways: (a) The rattle itself charms the prey by its attractive sound (Blumenbach, 1798, p. 252); or (b) the rattle draws the attention of the prey to the snake, whereupon it is brought within the influence of the rattler's hypnotic eye (Mead, 1745, p. 82; 1747, p. 82; S. Smith, 1765, p. 505; Wesley, 1770, vol. 1, p. 174; 1784, vol. 2, p. 35; Shaw, 1802, vol. 3, p. 322; Rivers, 1874, p. 508); or, (c) the prey is so startled by the rattle as to become paralyzed and thus an easy catch (Gillam, 1916, p. 132; Devoe, 1945, p. 484).

I have dealt elsewhere (p. 1252) with the myth of the rattlesnake's power of fascination, which, although still widely current, is entirely unsupported by modern studies. With regard to the part played by the rattle in the theories of fascination, the following comments are appropriate: The first and third of the proposals listed above are, of course, virtually antithetical; the rattle could not at once be both attractive and paralyzing. Blumenbach got his information from Major Gardner, of Florida, who stated that the Indians caught squirrels by imitating the sound of the rattle. Barton (1800, p. 13) reported that inquiries among the Indians had failed to verify this practice; he deplored the way in which European scientists were imposed upon by the tall tales of travelers.

The second of these subtheories requires a belief in the mythical power of the rattler to charm with its eye. Mead (1745, p. 82), who may have been the first to suggest this use of the rattle, did not claim that it was backed by field observation; on the contrary, he merely concluded that the rattle must be useful to the snake in some way and this was evidently its beneficial purpose. Others have believed in the power of fascination because they thought rattlers too lazy and slow-moving to capture prey by any other method than some form of remote influence, which overlooks their ability to ambush prey or to follow it down holes.

Finally we have the theory of the paralyzing sound, still believed by some. Curran and Kauffeld (1937, p. 52) were told by a naturalist that he had seen a rattler bring a bird to a standstill by sounding its rattle. One cannot state categorically that no bird or mammal was ever startled into immobility, but it is certainly extremely doubtful that the rattle is ever deliberately or instinctively sounded for this purpose. In the particular instance cited, assuming the observation to have been accurate, the snake may have rattled because the naturalist

disturbed it, rather than in an endeavor to halt the bird. Kunzé (1879, p. 309) has pointed out that the sound of the rattle does not produce fear in prey. Observations of captive rattlers indicate that if the rattle does startle the prey it is more likely to cause it to run or fly away than to be paralyzed with fear (see also Garman, 1883, p. xxvi).

The other theories assigning the rattle to the securing of prey are based on the premise that the rattle simulates the sound of the prey of some creature that the rattler seeks, such as the sound of the cicada that birds might hunt. That the rattle sounds much like some kinds of cicadas or locusts is unquestionably true, but that the snake actually buzzes the rattle to attract the birds is to be very seriously doubted, although suggested by several writers (Shaler, 1872, p. 33; Babcock, 1929b, p. 27). Fitch (1903, p. 315) thought the sound of the rattle to be like that of a bee and believed it would attract phoebes and king birds. Garman (1883, p. xxvi), Gillespie (1937, p. 132), and Ingersoll (1884a, p. 401) all doubt the cicada theory, either because the rattle is seldom heard in the wild, because rattlers seldom eat birds, or because the noise would tend to frighten rather than to attract the birds. Some authors have missed the point of the cicada theory, basing their disbelief on the fact that rattlers are not insect eaters (Lydekker, 1896, vol. 5, p. 242).<sup>3</sup>

Ingersoll (1884a, p. 401) thought that birds might be attracted to the sound of the rattle out of pure curiosity, but not because of a fancied resemblance to the sound of some insect. In a letter, the late A. M. Jackley expressed the same idea: "Under some circumstances the rattle does serve as a lure. It is not to be inferred that the snake, when on a foray, goes along shaking his rattles to attract his prey. I don't give them credit for that much intelligence. The facts are: When a chipmunk, horned lark, or other prey approaches a rattler, it is curious and disposed to investigate. Then the rattler, either from nervousness or design, gently shakes his rattles, and the bird or animal retreats only to become more keenly interested. Finally, their curiosity overcomes their fear and they throw caution aside, with fatal results."

E. G. Boulenger (1914, p. 185), although not advocating the theory himself, records the belief that the rattle may decoy thirsty creatures to their destruction because of the resemblance of the sound to that of running water. This is quite fantastic since there is no such resemblance. In conclusion, it may be stated that no experience with rattlers in the field or in captivity tends to encourage credence in any of the various prey-securing theories.

The question may be asked whether the rattler ever uses its rattle after the prey has been struck or while swallowing food. I have already mentioned C. B. Perkins' statement to the effect that a snake will sometimes twitch the rattle if another approaches while it is feeding or preparing to feed. Mole (1895, p. 190) thought a rattler would be all the more ready to rattle while swallowing prey because of its defenseless condition. Kunzé (1879, p. 309) noted that, when mice were fed to a rattler, in only 2 out of 40 times was the rattle sounded, and on both occasions the rattler was startled. Menger (1905, p. 13) came upon a rattler eating

<sup>3</sup> Charles Waterton, by some queer extension of this theory, thought the vibrating rattle *looked* like a pale green grasshopper and he was almost bitten when he tried to capture the insect (Aldington, 1949, p. 69). He doesn't say that it also *sounded* like one, but if it didn't, why did he fail to note the sound?

a brush rabbit and simultaneously sounding the rattle. We may presume that the snake had sensed his approaching footfalls. I was told of a general belief in Louisiana that rattlesnakes rattle to scare other creatures away, thus keeping them from stealing the snake's prey. But, summarizing, it may be said that feeding rattlers will not rattle unless disturbed.

Before proceeding to a discussion of the warning theory, one belief that misled the early naturalists must be corrected, this being the entirely erroneous idea that the rattle sounds involuntarily whenever the snake crawls—clearly the presumption of one who had never seen a live snake in action. This statement occurred in one of the first printed accounts of the rattlesnake (Magalhães, 1576, fol. 24<sup>r</sup>; Stetson, 1922, vol. 2, p. 63), and was repeatedly reaffirmed during 300 years (Purchas, 1625, vol. 4, p. 1304; Piso, 1648, p. 41; Jonstonus, 1653, p. 26; 1657, p. 23; Wynne, 1770, vol. 1, p. 42; Wesley, 1770, vol. 1, p. 173; 1784, vol. 2, p. 36; Goldsmith, 1774, vol. 7, p. 209; Clavigero, 1787, vol. 1, p. 59; Loskiel, 1794, p. 87; Fleming, 1822, vol. 2, p. 293; Holmes, 1823, p. 257; Murray, 1829, vol. 2, p. 316; Anon., 1832b, p. 99; Bigland, 1844, p. 136; and Unonius, 1950, p. 297).

A typical expression of this belief, so contrary to every field observation or laboratory test, is that of Magnin (1869, p. 360): "Imagine these [the rattles] constantly clattering against each other, as the reptile moves, with a hoarse, dull, echoing sound, and you will be able to form some idea of the permanent warning of its approach which the *Crotalus* carries about with it."

But as early as 1634, William Wood (p. 47) said: "... at her taile is a rattle with which she makes a noyse *when she is molested*" (italics mine); and the theory that the rattle sounds involuntarily whenever the snake moves was specifically denied by Mead (1745, p. 83; 1747, p. 83), followed by S. Smith (1765, p. 506), Beauvois (1799, p. 369), Ord (1815, p. 358), and Anon. (1872b, p. 642). Occasionally, the compromise statement is made that the rattle makes some noise as the snake travels, but much more when it is annoyed (Zeisberger, 1910, p. 70, but written in 1779–80; Good, 1853, p. 5). There is an element of truth in this, for although a rattler crawling at a normal gait makes no sound with the rattle, if it be terrified into thrashing along as fast as possible through brush and rocks, the rattle may occasionally strike some obstruction and be audible as a click. But this is far from the strident hiss of the deliberately sounded rattle; and any thought that the rattle can be heard as the snake goes about its ordinary affairs is completely incorrect.

Finally we come to the real purpose of the rattle, namely, its use as a warning—not a warning addressed to prey, nor the altruistic warning of the intruder for the intruder's protection, but a warning or threat intended to drive away creatures that might harm the rattler itself.

When we consider these many theories that have been suggested to explain the fundamental purpose of the rattle, it is at once apparent that the usual rattlesnake reaction, which is almost universal, gives strong support to a single theory in preference to all others. For what does any rattlesnake do with its rattles? It sounds them when disturbed or frightened, as by some movement or the approach of an intruder. Upon this there can be no argument; it is the common experience of everyone who has encountered a rattler in the field or startled one in cap-

tivity. I have no desire to assume an irritating attitude of assurance, but certainly I have seen this happen a thousand times; and there are others of more extensive experience who corroborate this observation.

The rattle is used as a warning signal; upon this, experience permits no argument; if it has alternative purposes, such as those previously mentioned, the burden of proof is upon those who advance them, for they are not matters of daily observation. The "keep-your-distance" use of the rattle is so universal and instinctive that one would suppose this problem of use to have been long since settled; and I might well be accused of giving undue importance to a nonexistent argument, were it not for the fact that books continue to appear, attributing to the rattle as much uncertainty of purpose, or diversity of use, as did the popular natural histories of a century ago (e.g., Berridge, 1935, p. 337; Ditmars, 1936, p. 62; Gillespie, 1937, p. 132; Curran and Kauffeld, 1937, p. 51; De Lys, 1948, p. 73; Moore, 1951, p. 229. See also Huxley's reply (1939, p. 725) to the criticisms of his advocacy of the warning theory). And it must be admitted that the nature and purpose of the warning have sometimes been so misinterpreted as to throw the theory into doubt and disrepute.

The warning theory is very old,<sup>4</sup> but from the first it has been, and still is, a matter of argument because of a confusion, often unrecognized, between three types of warning: that is, the warning of (1) intruders, possibly dangerous, warned for the protection of the snake; (2) intruders warned for the protection of the warnee, instead of the warner; or (3) prey, the last being a special case, already discussed, of (2). If we sharply distinguish between these three and point out the manner in which the rattle is beneficial to its possessor, by frightening away creatures that might otherwise injure the snake, we at once eliminate the objections which have been so often advanced against the warning theory. Certainly no animal will warn away the food upon which it depends for subsistence, or develop so intricate a mechanism for the altruistic protection of the innocent passer-by. But it is equally clear that warning devices that tend to safeguard their owners are common in nature; and there is no more reason to question the purpose of the rattle than that of these other devices. It is only necessary to show that the rattle is used for this purpose, is often effective, and that its disadvantages are not so important as have sometimes been supposed.

I shall give no further attention to those arguments against the warning theory that are based on this confusion between a beneficial warning, and one neutral or injurious to the rattler. Darwin himself tried to correct this confusion many years ago, with indifferent success; in fact, his position is still occasionally ad-

<sup>4</sup> As evidenced by the following expositions appearing before 1700: Hernández, 1615, fol. 192<sup>r</sup>; 1628, p. 329; 1651, p. 329; Wood, 1634, p. 47; Nieremberg, 1635, p. 269; Piso, 1648, p. 41; Clarke, 1670, p. 42). It has been supported by many subsequent authors; I omit the citations because they are so numerous, not because the theory has fallen into disrepute. One of the most succinct statements is that of Hornaday (1904, p. 348): "He rattles to save himself from injury, and his persistent *whirr* has saved thousands of persons, and tens of thousands of domestic animals, from being bitten. A western cow-pony, a government mule, or a range steer will spring sidewise from a warning *whirr* in the sage-brush quite as quickly as man himself, and almost as far." Or as put by HENDERSON (1872, p. 261): "I am a rattlesnake, armed with what will be death to you if you come too near; give me a wide berth." Another well-stated exposition of the theory is that of Huxley (1938, p. 15). When Zimmermann and Pope (1948, p. 357) prefer to consider the sounding of the rattle as a *bluffing* rather than a *warning* reaction, it seems to me they fall into a serious semantic error; the hiss of a gopher snake is a bluff, for it has no important weapon in reserve. But the rattler can follow its warning with a really dangerous strike.

vanced (e.g., Curran and Kauffeld, 1937, p. 51) as an argument against the theory, notwithstanding his clear statement in advocacy of it.<sup>5</sup>

As I have stated, the validity, in terms of adaptive value, of the dangerous-enemy warning theory may be presumed to rest with the answers to these questions:

- (1) Is the rattle used as a warning?
- (2) Is it effective?
- (3) Does it ever react against the rattler, and if so, to what extent and under what conditions?

On the first point I think enough has been said: The rattle is so used—this is the reaction that anyone familiar with these snakes invariably expects when he approaches one.

Is it effective? The answer, of course, depends on the circumstances, as it would were we discussing the growl of a dog, the hiss of a gander, or the earth-pawing of a bull. These are all warning reactions, and they may result in success or failure, depending on the character and purpose of the trespasser. They may be followed by more direct action or by the retreat of the warner.

One of the mistakes made by early writers, and repeated in later natural histories, is in the general characterization given the rattler's warning posture. Usually the snake is portrayed in its resting coil with rattle sounding. To the possible inadequacy of such a warning mechanism one may agree, but this is not the entire story by any means. Just as the cat arches its back, fluffs its tail, opens its mouth, and spits and squalls, so the rattler has more than a single warning reaction. It is true that a snake found in its resting coil may first sound the rattle without changing position. But if this preliminary warning fails to halt the trespasser, it quickly adopts more spectacular methods, which concurrently place it in a better position either for defense or escape. For now, still sounding the rattle furiously, it raises the anterior part of the body above the ground in an S-shaped spiral, with the head and neck held like a poised lance ready for a forward lunge; the posterior part of the body is flattened to stabilize the anchorage or to facilitate mobility; the tongue, with tips widely spread, is protruded to the utmost and is alternately pointed vertically upward and downward with intervening pauses; and the snake inhales and exhales with a violent hiss. Now the rattler is ready for whatever may come; it can strike, if the enemy comes within range, or it can retreat (still facing the intruder) toward the nearest rock crevice or bush that might serve as a refuge. In this composite picture, the rattle serves as the alarm bell.

<sup>5</sup> "It is admitted that the rattlesnake has a poison fang for its own defense and for the destruction of its prey; but some authors suppose that at the same time this snake is furnished with a rattle for its own injury, namely, to warn its prey to escape. I would almost as soon believe that the cat curls the end of its tail when preparing to spring, in order to warn the doomed mouse." *Origin of Species*, first ed., 1859, p. 201; fifth ed., 1871, p. 196.

As a result of criticism, particularly from St. George Mivart (1871, p. 50), Darwin clarified the statement in the subsequent editions of the *Origin*: "Some authors suppose that at the same time it [the rattlesnake] is furnished with a rattle for its own injury, namely, to warn its prey . . . It is much more probable that the rattlesnake uses its rattle, the cobra expands its frill, and the puff-adder swells whilst hissing so loudly and harshly, in order to alarm the many birds and beasts which are known to attack even the most venomous species. But I have not space here to enlarge on the many ways by which animals endeavor to frighten away their enemies." *Origin of Species*, sixth ed., 1885, p. 162. But even this statement has not prevented his being cited as opposing the warning theory, when, in fact, he opposed only the misinterpretation of enemy warning into prey warning. See also Darwin (1873, p. 107) and Wallace (1890, p. 262).

When a rattle is heard in such circumstances, no prior experience or mental process is necessary for a realization of threatened danger; both the stridency of the sound, and the other actions of the snake to which the sound draws attention, will have an immediate effect on any creature capable of the most elementary reactions of self-protection, impelling caution or retreat. Several of the early writers (Rees, 1819, p. [1]; Brainard, 1855, p. 124; Wood, 1863, vol. 3, p. 101) attribute to the noise of the rattle an effect mysterious in its action, in that animals having had no previous experience with it—a reaction said to be exemplified by that of the European horse—seemed fully aware of its purpose, and recoiled instinctively from the sound. Although the factor of molestor-experience may have had some bearing on the genesis of the rattle, as is discussed hereafter, we need no longer consider such experience necessary, especially when this startling sound begins suddenly and unexpectedly under one's very feet. But the effect of the warning is by no means dependent entirely on the initial surprise, so strident is the noise, and so alarming the other actions of the snake. Baillie-Grohman (1882, p. 105) cites his own experience as a tenderfoot. Using his hands to climb a rocky peak, he had his attention suddenly drawn by the noise of a rattle to a creature whose like he had never seen before. He didn't know it was a rattlesnake, but it "looked so venomous" that he backed away and fell down the cliff.

In judging the effectiveness of this warning as a means of protection, one must have in mind the kinds of carnivores and birds of prey that seek the rattler as food, and the ungulates that might tread on it fortuitously, or with destructive purpose. Against many of these, such as wolves, coyotes, bobcats, and the like, the rattle would be a valuable protective adjunct—not unfailing, of course, but still of major importance in frightening these creatures into looking elsewhere for a meal. One has only to watch the reaction of a dog or cat with a rattler to see how effective this is, despite the qualification that some of them become experienced rattler killers (p. 1074).

Cowles (1938, p. 16) observed that western skunks were driven from their customary feeding grounds by the sounds of the rattle. Cowles and Bogert experimented with a weasel and found that it would not attack a sidewinder while the latter possessed and sounded its rattle, but did attack when the snake's rattle had been removed. Jeter (1854, p. 9) made the observation that most animals scamper off when they hear the sound of the rattle. Hawks, owls, and ravens might be similarly frightened.

As to the larger herbivorous mammals, they are not usually of such a disposition as to go out of their way in search of trouble, although deer and antelope do show an inclination to attack rattlers by jumping on them (p. 1065). Judging from observations of the reactions of horses and cattle it is quite evident that the rattle has a definite protective value. A. M. Jackley recounted the following somewhat typical incident: "One fall I parked my car on the edge of a small prairie-dog town to watch the rattlesnakes as they arrived to hibernate. About 30 rods beyond my car was a large Hereford bull. This bull was of a friendly sort and started walking toward me. It happened that a large rattler was lying still, in thin grass about 60 feet in front of me and directly in line of the bull's approach. When the bull came to within about 15 feet of the snake it coiled and rattled, and the bull stopped—and then leisurely detoured and came to my car.

My conclusion was that this snake rattled because it was afraid, and the bull detoured for the same reason. No doubt, in case a rattler is approached by a potential enemy, the elements of both fright and anger are manifested by the rattling."

Although some writers (e.g., Rees, 1819, p. [1]) speak of animals being shocked into immobility, while others (e.g., Bigland, 1844, p. 136) say they are driven to flight, it is probable that most of them simply adopt a policy of avoidance, as did Jackley's bull. Horses sometimes shy at rattlers, but the reaction is by no means so universal as some of the earlier natural histories indicated (p. 989). However, they do tend to avoid a snake that suddenly rears and rattles in their path.

Summarizing this phase of the theory, it may be concluded that the rattle is of definite adaptive value when sounded as a warning to animals which, with intention or unconsciously, might injure the snake.

We come now to the third query: Is the rattle ever a detriment by advertising the presence of the rattler to potential enemies, from which it might otherwise escape?

It has been pointed out that the use of the rattle may serve only to invite destruction by certain animals, such as deer and hogs, which do kill rattlers upon occasion (p. 1065). For example, Berridge (1935, p. 62) considers this a fatal flaw in the warning theory. Now certainly this would be true if the rattle served to invite destruction by advertising the snake's presence, when inconspicuous inactivity, or a silent withdrawal would be a safer policy. This, however, misjudges the rattler's ordinary sequential response to the presence of an intruder. No field collector knows how many rattlers he may pass, that escape by merely lying quiet. But I have spied enough of them, fully aware of my presence, yet making no sound or movement, except possibly a telltale flicking of the tongue, to realize that they will depend on this method of escape whenever possible. The rattle is the reaction of a suddenly startled snake, or of one aroused to action by the persistent encroachment of an enemy.

This criticism also misjudges the reaction of animals to the sound of the rattle. They are pictured as saying to themselves when they hear it, as a man would, "Here is a dangerous creature that I had best destroy, for the safety of others who may pass this way." But no wild animal reasons thus; there is always a more specific purpose in attack, such as a desire for food or the protection of young. Against such creatures, keeping in mind the fact that the rattle is not sounded until procrypsis has failed, its possession is definitely protective, for it often causes them to turn aside and avoid the snake.

With man, an enemy who can destroy at a distance without endangering himself, the rattle is a disadvantage, as was pointed out as early as 1871 by Cope (p. 120). For man is poorly equipped with senses, and the rattler may sometimes advertise itself too quickly when it might otherwise lie undiscovered. But this is no valid argument against the adaptive value of the rattle as a warning mechanism, since rattlers long antedated man in the New World, and the rattle was developed without regard to the novel conditions imposed by this addition to the local fauna. It has even been suggested that man is beginning to exercise a reverse evolutionary effect on the use of the rattle:

The people hereabouts say rattlesnakes are getting scarcer. Some claim the rattlers do not buzz at the slightest provocation as they formerly did, and advance the argument that the "buzzers" in the past were the ones killed, the quiet snakes ordinarily making their escape. *Everett Jensen, U. S. Forest Service, Sawyers Bar, Calif.*

We may thus summarize our conclusions with respect to the warning theory: The rattle is used as a warning; it is often effective; detrimental results are unusual and rare, particularly in the case of the fauna indigenous to the areas where rattlesnakes occur. Thus the validity of the warning theory of the function of the rattle is proved by observations of the conditions and situations wherein it is used, and by its apparent value to the user in these situations, thereby furnishing a basis for its adaptive development.

In connection with the expositions of the warning theory, there have been criticisms of too direct an implication of intent upon the part of the rattlesnake when it sounds its rattle (Maier and Schneirla, 1935, p. 222; Verrill, 1937, p. 30). It is difficult to describe the variability in the several elements of a rattlesnake's reaction to an intruder without some anthropomorphic implications, for there is definitely some choice in the duration and sequence of these elements. Various external conditions, of course, affect the reaction, such as the temperature, the visibility, and the availability of a refuge. But, besides these external stimuli, there are not only species and age differences in the rattlers and their reactions, but also individual differences as well. These are shown in the adoption and timing of the several reactions of procrypsis, threatening defense, flight, and even, rarely, attack. The extent to which this choice may have a psychological basis I do not know, but I should willingly concede that the snake has no purposeful knowledge that his threatening defense may save him from an intruder. And as to the tail vibration that produces a sound he cannot hear, this is only one part of a composite defense posture, which includes the S-coil, the flattened body, the deep breath and hiss, and the spread-tipped tongue, alternately erected and depressed. As a part of this composite program, sounding the rattle is simply a nervous reaction, almost automatic, to a frightening situation. But the fact that the snake has no realization of the effect produced, either by intent or otherwise, does not weaken the conclusion that the warning theory can explain, as no other can, both the adaptive value of the rattle and the circumstances of its present use.

A few matters related to the warning theory remain to be touched on, besides its effect on the theory of the evolution of the rattle, to which I shall later return.

Garman (1883, p. xxvi; 1888, p. 264; 1889, p. 177) and Taylor (1892b, p. 354) think that the warning is important in relieving the rattler of the necessity of using its venom on its enemies, thus improving its ability to secure food. It also conserves the fangs.

There have been extensions of the warning theory into the realms of fantasy. Paine (1875, p. 135) reports that the jingle of the rattle soothes the black snake to such an extent that its intended attack on a rattler is abandoned. Bernard (1887, p. 223) said that when a Negro imitated a rattler, two harmless snakes in his cabin fled. De Lys (1948, p. 73) thought one purpose of the rattle was to let enemy snakes know that a rattler was present. As snakes are deaf to air-borne sounds, these yarns are completely incredible.

Meek, with his usual flair for invention, reports (1946, p. 162) that the human

ear cannot stand the sound of the rattle for any length of time. I have withstood it for an hour or so, although admittedly it becomes somewhat trying if one wishes to concentrate on scale counting, or some other laboratory task. Wood (1855, p. 332) tells the story of a man who kept track of a rattler's location by throwing sticks and stones at it from time to time to keep it rattling, so that it would not catch him unaware while he was at work. He fails to state why the man did not kill the rattler and go on about his business.

#### THE ORIGIN OF THE RATTLE

Theories of the origin of the rattle are necessarily related to the theories regarding its present use. Also such theories touch on two phases of the same problem, namely, why the mechanism was evolved, and how it was evolved, as a complicated appendage, from the simple tail cone of the common ancestors of the rattlesnakes and their rattleless relatives.

The earliest theories of the genesis of the rattle, in line with the accepted precepts of individual species creation, visualized the rattle as having been created in its present perfected form, the work of a Divine Providence desirous of protecting innocent creatures from this dangerous and malevolent snake (Glover, 1676, p. 631; Lawson, 1709, p. 128; Carver, 1778, p. 480; Dobrizhoffer, 1784; 1822, vol. 2, p. 287; Bingley, 1803, vol. 3, p. 71; Bigland, 1844, p. 136. See also Thwaites, 1896-1901, vol. 43, p. 155, for a similar statement by a Jesuit priest in 1658). This theory was usually the accompaniment of the erroneous belief that a rattler involuntarily sounds its rattle whenever it moves, regardless of whether it has been annoyed or disturbed.

Linking the rattle development to modern theories of evolution, premised on its use as a warning primarily beneficial to the snake itself, usually assumes the ancestors of the rattlers to have lived in a prairie country inhabited by herds of hoofed animals akin to the modern bison. "The hoofs of these ponderous animals, traveling over the plains, must have been distinctly dangerous to snakes living in the open, while the snake's bite would be distinctly unpleasant to the bison, although death would probably have rarely ensued owing to the beast's great bulk. The bison would gladly keep out of the snake's way, however, if warned, and this warning the rattle gave" (Barbour, 1926, p. 41; 1934, p. 42). This relationship of the warning theory to the origin of the rattle was first suggested by O. P. Hay (1887, p. 214), and was reiterated by Garman (1889, p. 176). Barbour (1922, p. 37) points out a possibly similar derivation of the venom-squirting ability of the spitting cobras of Africa as a protection against the great herds of antelope on the veldt. However, in this case the fine stream of venom reaching the antelope's eyes is, in itself, painful and even dangerous, while the rattle is only a threat of worse to come.

Curran and Kauffeld (1937, p. 52) express doubt as to the bison theory because rattlesnake remains have not been found commingled with bison fossils. This is hardly valid, in view of the great difference in the preservability of the remains of the two creatures. Because of the delicacy and fragility of their bones, rattlesnake fossils are quite rare. K. P. Schmidt (*in litt.*) believes that the rattlesnake group evolved in North America during the major evolution of large mammals, both herbivores and carnivores.

It is generally agreed that the rattle arose as a specialization—a sound-producing implementation—of a common snake reaction, namely, that of vibrating the tail when angered or annoyed. This method of threatening or bluffing is so widespread, being used alike by venomous and harmless snakes, and by many unrelated kinds of snakes throughout the world, that it must have been an exceedingly primitive development. It has been known to man since the earliest days, for anyone who ever handled snakes has quickly become familiar with this universal ophidian way of saying, "Look out; I'll bite if you come within reach." Some snakes, vibrating their tails among leaves, achieve a tolerable imitation of the sound of a rattler's rattle; however, this can hardly be construed as purposeful or adaptive simulation, as the tail-vibration must have antedated the development of the rattle and it is equally prevalent in the Old World, where there are no rattlers to imitate.

That the rattle developed as a specialization of the cone that terminates the tail of most snakes, there can be no doubt. One can easily visualize how, by a constriction at the base, successive sheddings would be retained on the terminal cone, thus thickening and toughening it. Garman (1892, p. 16) thought that two genera of lizards have the spines on their dorsal crests toughened by the retention of successive sheddings. Also in earlier works (1888, p. 266; 1889, p. 177), both through studies of the embryology of the rattlesnake, and the developing and adult tail spines of related species, he has shown how a primitive type of rattle might have been evolved.

Quelch (1891, p. 10) has suggested that the rattle might have been developed by snakes living in rocky situations, where their tails required thickening to withstand wear when they were vibrated. Curran and Kauffeld (1937, p. 53) have proposed an even queerer evolutionary twist "an unusually large spine at the tip of the tail . . . might well have prevented the complete casting of the skin and necessitated the development of the rattle." This implies that the rattle has a nuisance rather than a beneficial value. Cope (1871, p. 108; 1887, p. 197) explains the development by inferring that an increased use of the vibrating tail would tend to localize growth-nutrition, thus resulting in an improved structure. It is an explanation that merely transfers uncertainties.

It is probable that Garman's theories of evolution are substantially correct, but it has to be admitted that there must have been many intricate steps between the mere retention of successive sheddings on the tail cone, and the perfection of the highly complicated mechanism whereby each such successive slough is shifted backward one lobe with the accretion of each new one, thus giving the loose fit required in the noise-making apparatus. We can only speculate as to the course this development may have taken, for we have available for study neither partially developed mechanisms of this type in other kinds of snakes, nor the assistance of embryology, since the rattle-shifting procedure is a postnatal development. It is, indeed, a long jump, with an unknown gap, from a multiple-thickness tail spine to the highly intricate rattle, with its several lobes and other perfected details of structure.

Whether the rattle is developing further evolutionary changes today, we cannot say. At least two small species, the pigmy rattler (*Sistrurus miliarius*) and the long-tailed rattler (*Crotalus stejnegeri*) have rattles so tiny as to be almost valueless

as sound producers, but whether these rattles are primitive or on the way toward elimination we have no way of knowing. Curran and Kauffeld (1937, p. 53) are incorrect in stating that the rattle of the tropical rattlesnake (*C. d. durissus*) may be disappearing, as the rattles are much reduced in size. This snake has unusually small rattles when young—small in proportion to the size of the snake—but the rattles of the adults are as large or larger than in other species of corresponding size.

Garman (1888, p. 267) visualized the rattle as having developed separately in the two genera *Sistrurus* (characterized by plates on the crown of the head) and *Crotalus* (having scales on the crown). Stejneger (1895, p. 392) dissented from this view of separate derivations of the genera. As a matter of fact, this distinction between the genera is not as sharp as these definitions imply. Some individuals of *Sistrurus* have sutured plates; and some species of *Crotalus*—*durissus*, for example—have enlarged scales on the crown that approach the *Sistrurus* plates in form. Evolutionary trends from the nine typical plates of the Colubridae toward a break-up into many scales are common in various groups of snakes. It appears sounder to visualize this type of evolution as occurring among the rattlesnakes after the acquisition of the exceedingly complicated rattle mechanism, rather than to assume that the rattle was developed twice in two separate lines of descent—once in *Sistrurus* from *Agkistrodon*, and again in *Crotalus* from *Bothrops*. The matter is discussed further under phylogeny, p. 152.

#### CONDITIONS OF USE

The conditions under which a rattlesnake will sound—or fail to sound—its rattle as a warning, have been discussed elsewhere (p. 469). It has been pointed out that it is by no means invariably sounded prior to a strike, as is often thought to be the case—a widespread belief that should be strongly discouraged in the interest of safety. For whether a rattlesnake will rattle when disturbed, before undertaking a more retaliatory defense, depends on a number of conditions, such as the species and the individual temperament of the snake; the suddenness with which the intruder comes upon it, and the closeness of his approach; whether the snake was startled out of sleep; whether an injury to the snake was involved; the temperature; the availability of hiding places; and other, similar variables. No one can guess a snake's course of action in advance. It will usually rattle before striking, if the danger is not too imminent to permit delay; but surely no one is justified in depending on the rattle as a trustworthy or invariable advance note of caution.

Although the S-shaped defensive coil is the usual position of a rattling snake—this being a part of the general defensive posture of which rattling is another element—it can rattle when outstretched, either at rest or crawling.<sup>6</sup> It often rattles while trying to escape to some nearby refuge. Disturbed snakes may sometimes be heard rattling in the restricted confines of a hole or rock crevice.

Annoyed snakes can rattle for long periods without rest. Ingersoll (1884a, p. 401) stated that he witnessed their rattling for several hours without a moment's interruption. Perry (1920, p. 85) reported a timber rattler (*C. h. horridus*) that

<sup>6</sup> Under no circumstances should this statement be misconstrued as meaning that a rattler involuntarily makes a noise with its rattles when crawling, a mistaken presumption by early writers who had never seen a live rattler in action.

rattled for half an hour, and Hylander (1951, p. 66) an eastern diamondback (*C. adamanteus*) that rattled for an hour. I have never made any accurate records of long runs, but in the laboratory, when endeavoring to concentrate on scale counting, I have frequently found it necessary to remove live specimens, so annoying is the continuous rattling of especially nervous snakes not yet accustomed to captivity.

Many conditions affect the distance at which a rattler may be heard—the size of the snake more than any other—which explains some of the conflicting accounts that have been published. Another important qualification is the length of the rattle string. As indicated elsewhere a string of about 6 to 8 segments is probably most efficient as a sound producer; too short a string produces too few contacts for full stridency, while the outer segments of extra-long strings interfere with, or damp out, the full vibrations of the segments next the tail.

The distances at which the sound of the rattle may be heard have been variously reported as follows: Lindeström (1655; 1925, p. 186) 100 ells or about 225 feet; Jesuit priest in 1658 (Thwaites, 1896–1901, vol. 43, p. 153) 20 paces; Holm (1702; 1834, p. 53) 100 yards; Lahontan (1703, vol. 1, p. 242) 30 paces; Daudin (1801–4, vol. 5, p. 299) 60 feet; Bosc (1803, p. 552) 12 to 15 feet; Shaler (1872, p. 33) 100 feet; Flack (1866, p. 316) 100 feet; Mivart (1888, p. 293) 10 to 20 yards; Garman (1889, p. 177) 8 rods; Ritter (1921, p. 30) 80 paces; Anderson (1951, p. 8) 160 yards; Herrick (1953, p. 23) 10 yards.

Ross Allen reports that a large eastern diamond rattler with a string of 16 rattles could be heard 105 feet when there were no obstructions and no wind. Against the wind it could be heard between 25 and 40 feet.

One of my correspondents reports:

Two rattlers were found at the edge of a gopher hole, along a fence line where rocks were scarce and the grass was grazed short. They started rattling so we could hear them when we were 700 feet from them. The distance is fairly accurate because I was working as a chainman surveying a line along the fence when I found them. *C. K. Lyman, Newport, Wash.*

Another said that a large western diamond (*C. atrox*) could be heard 200 feet away.

Several writers comment on the greater danger from the pigmy rattler (*S. miliarius*) because its tiny rattle can hardly be heard at all (Say, 1819, p. 263; Tixier, 1844; 1940, p. 76; Robinson, 1896, p. 711). A correspondent advised me that this little snake could not be heard beyond 5 feet. Allen and Neill (1950b, p. 10) give the distance as "a few yards." However, it should also be mentioned that the minute size of the snake, with its meager supply of venom and short fangs, greatly minimizes any danger from it, regardless of the slight audibility of the rattle.

I experimented in a closed room with adults of three species of rattlers having notably small rattles. A long-tailed rattler (*C. stejnegeri*) was audible at from 4 to 6 feet. One central-plateau dusky rattler (*C. t. triseriatus*) could be heard at 10 feet, but only if attention were focused on it. Certainly it would not have attracted attention at that distance. Another individual could not be heard beyond 4 feet. The rattle of an Omilteman small-headed rattler (*C. i. omiltemanus*) was audible as a faint buzz at 7 feet. It is evident that such rattles as these tiny affairs have retained little value as warning devices.

Rivers (1874, p. 507) says it is not easy to locate an invisible rattler from the sound, as it seems to come from all directions. There is probably an element of truth in this, although the ventriloquistic effect is not conspicuous unless there are intervening rocks or shrubbery. Fox (1948, p. 63) was unable to tell at first where the sound was coming from, when he stepped on an eastern massasauga (*S. c. catenatus*) that continued to strike vainly at his boot.

Much has been written of the variations in the sound of the rattle that a rattlesnake may produce at will—a “variety of cadences” in the words of Hopley (1882, p. 312). While the speed of vibration has been shown elsewhere (p. 241) to be largely dependent on temperature, it is probable that the snake has some control over both the frequency and the amplitude of vibration, and therefore of the tone and intensity of the sound. That there is some degree of control over this intensity can be proved if we aggravate the annoyance of a snake that is already rattling, thus causing it to increase its muscular activity. However, most of the varying sounds attributed to the rattles are exaggerated or fictitious, being cited to prove a duality of rattle use that does not exist. Crèvecoeur (1782, p. 240; 1783, p. 101; Bingley, 1803, vol. 3, p. 75) said the sound of the rattle is loud and shrill when the snake is angry but faint when it is pleased. Nicholson (1877, p. 266) had one in captivity that could play several different notes indicative of anger, pleasure, or loneliness. Garman (1883, p. xxvi) said the rattle was used energetically to indicate anger, but softly as a mating call. Rutledge (1932, p. 53) said he watched two undisturbed rattlers softly signaling to each other. But Flack (1866, p. 316) and Ingersoll (1884a, p. 403), on a more realistic plane, noted only that the loudness of the sound varied with the degree of the snake’s anger or apprehension. Kunzé (1879, p. 309) thought that snakes rattled louder in hot weather. It is now known that the speed of vibration increases with higher temperatures.

Crites (1952, pp. 54, 62) believed a rattlesnake able to sound three cadences with the rattle: first, an alarm; secondly, a milder sound when crooning to its young; and, finally, a conversational tone when mating. As mother rattlesnakes do not remain with their young, and mating rattlers do not rattle, there is no verification of these variations in sound for different purposes.

It is commonly observed of captive snakes that many of them—perhaps a majority—become so accustomed to the presence of people that they must be deliberately annoyed to be made to rattle. In fact some wild rattlers, particularly red diamonds (*C. r. ruber*), will often rattle only after being prodded with a stick.

Since Dudley first stated in 1723 (p. 293) that the Indians were afraid to traverse the woods in wet weather because the rattlers’ rattles would be inaudible, the story has been often repeated (Kalm, 1752–53, p. 316; Pennant, 1787, p. 88; Lacépède, 1788–89, vol. 2, p. 412, Kerr, 1802, vol. 4, p. 267; Winterbotham, 1795, p. 406). It may be doubted whether such expert woodsmen as the Indians were really influenced by this supposedly increased danger. Others who have commented on the added hazard resulting from wet rattles (but not necessarily as a hazard to Indians) have been Wesley (1784, vol. 2, p. 37), T. Smith (1806–7, p. 84), Wuerttemberg (1835; 1938, pp. 133, 275), LeConte (1858, p. 664), Nicholson (1877, p. 266), Cheney (1886, p. 185), Adair (1930, p. 62), Gowanloch (1934, p. 8; 1943, p. 57), Gharpurey (1935, p. 154), and Jackley (1946a, p. 1).

As a matter of fact, there is a considerable variation in the degree to which the rattles are muffled by dampness. When the snakes have been swimming, with the rattles under water—those that I have watched made no attempt to keep the rattles above water, as often reported—they usually become so water-soaked that they make little noise until they have had an opportunity to dry out or until the water has been thoroughly shaken out of them. This is particularly true if the snake, by rattling in the water, has caused the lobes to become filled, through the interstices between them.

Adair (1930, p. 62) thought that shedding also interfered with the snake's ability to rattle, but it seems to have little effect. Actually, a snake whose sight is hampered by the blue-eyed stage of shedding may be the more likely to rattle upon sensing an intruder.

R. E. Gordon wrote me of a belief in Georgia to the effect that rattlers lay their heads on their rattles when sleeping to keep the dew from dampening them. Another myth, of which I was told by Major Chapman Grant, is that rattlers will not rattle after dark, a yarn in which no credence will be placed by anyone who has hunted them at night.

#### RATTLE NOMENCLATURE

Some of the misunderstandings and doubts that have arisen regarding rattle development and structure, have been caused by a lack of consistency in terminology. To facilitate the discussion that follows I shall list the usages currently applied.

The complete caudal appendage of the rattlesnake is called the *rattle*, although it may alternatively be referred to as the *rattle string* to distinguish the entire set from the several parts, each of which may be referred to as a *rattle*. To avoid this possible source of misunderstanding it is probably best to use the term *segment* for the individual parts of a rattle. The segment, in turn, comprises from one to three (occasionally four) *lobes*; three lobes constitute each segment of most adult rattles. An alternative name for a lobe is a *ring*; however, this has also been used as synonymous with segment, for which reason I do not favor the term. The segment joining the string to the tail of a rattlesnake may be referred to as the *proximal*, *anterior*, or *attached* segment, that at the opposite end being the *distal*, *posterior*, or *terminal* segment (figs. 5:1 and 5:2). The posterior is the oldest remaining segment, and the anterior is the one most recently formed. When a proximal or attached segment is replaced by a new attached segment, the former becomes a *cast* segment.

Viewed in a transverse cross section, rattles have a wide and a narrow dimension. The broad side may be referred to as the *vertical* or *lateral* face; while the narrow side is the *horizontal*, *dorsal*, or *ventral* face. The *length* of a rattle, a segment, or a lobe, is the length measured in the direction of the axis of the snake; the *width* of a segment is presumed to be the maximum distance across its largest, or exterior lobe, measured across the vertical aspect, that is, from the dorsal (top) to the ventral (bottom) of the lobe. This may be more particularly defined as the *dorso-ventral* width (fig. 5:2).

The *prebutton* is the segment that comprises the entire rattle that the snake has at birth (fig. 5:3). This is invariably shed and lost with the snake's first exuviation a few days after birth; it is never retained as a part of the permanent string.

The *button* is the first retained rattle (figs. 5:1, 5:4, and 5:5); it invariably comprises the posterior segment of every rattle string, provided the string is complete. No term has been more misunderstood. Occasionally the word button has been used to designate the proximal segment, because this "buttons" the string to the snake's tail. More often it is used to designate the posterior lobe of the distal segment of a string regardless of whether or not the string is complete (Bumpus, 1885, vol. 3, p. 398). Under this terminology every string comprises "blank rattles and a button." Curran and Kauffeld (1937, p. 48) use the term button as interchangeable with segment, thus adding to the confusion. I shall use it only to

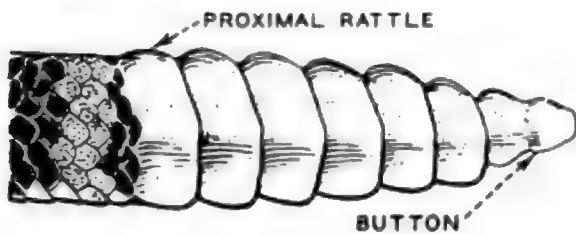


Fig. 5:1. Rattle terminology—a complete string.

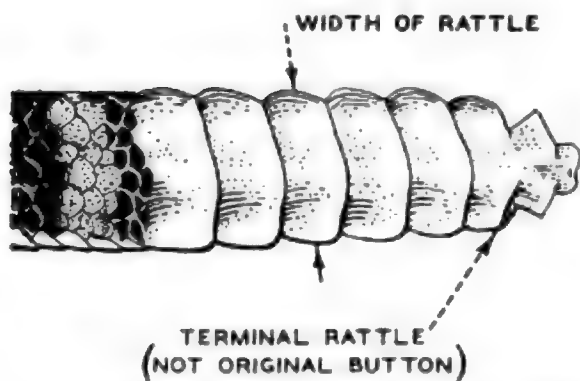


Fig. 5:2. Rattle terminology—a broken string after the loss of several segments; showing also the method of measuring the width of a segment.

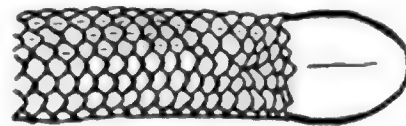


Fig. 5:3. A prebutton.

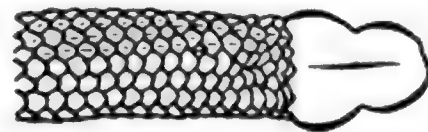


Fig. 5:4. A button.

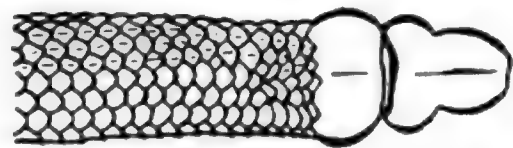


Fig. 5:5. A rattle-string comprising a button and a No. 2 rattle.

indicate the first permanent segment acquired by a snake, that is, the distal segment of any complete string. By a *complete* string is meant any string from which no segment has been separated by breakage or loss, subsequent to the invariable loss of the prebutton. The earliest use of the term button that I have found, is that by Holley in 1836 (p. 104).

The corrugated and hidden tip of the rattlesnake's tail, upon which the rattle is formed, has been termed the *end-body* by some, but I prefer *matrix*. The coalesced bony structure, the termination of the snake's vertebral column within the matrix, is usually termed the *style* or *shaker*. Zimmermann and Pope (1948, p. 363) define the several layers of the matrix as comprising the *epidermis*, *derma*, *connective tissue*, and *style*.

The *rattle-number* is the serial number of any segment in a complete string, beginning with the button as rattle No. 1, the next as No. 2, etc. Rattle-numbers can be determined positively only if a string is complete. In keeping records of

the condition of the rattle strings on individual snakes, I use such designations as 6+ or 9c, the first indicating an incomplete string of 6 rattles, the second a complete string of 9 rattles. Occasionally such figures as 7 + 1c may be used to indicate a string from which it is apparent that only one segment has been lost. As pointed out elsewhere (p. 310), it is not often that one can be sure how many segments have been lost; it is rarely safe to make a guess from dimensional data, if more than two are missing. I see no advantage in the more complicated rattle numbering system adopted by Woodbury and his associates (Heyrend and Call, 1951, p. 29).

The material of which the rattle is composed (*keratin*) becomes hardened or hornified by the process known as *keratinizing* or *keratinization*.

#### THE CHARACTER OF THE SOUND

The term "rattle" is to some degree a misnomer, when applied to the noise made by a rattlesnake; for "rattle," by definition, implies discontinuous or discrete sounds, whereas the separate sounds emanating from a snake's rattle are much too closely spaced to be perceived by the human ear. The result is a toneless<sup>7</sup> buzz, or, in the case of the larger snakes, a strident hiss. Hogan (1950, p. 9) well refers to the sound as a "siss."

Without mechanical means, such as an electric vibrator, it is quite impossible to imitate, by shaking a snake's rattle, the sound made by a live snake, for one cannot approach the snake's speed of vibration. In the early days, before live rattlesnakes were brought to Europe, people assumed that the rattle sounded in nature like the noise made by one shaken in the hand, and this led to deceptive ideas that were long prevalent. As early as 1658, a Jesuit priest correctly observed that it was impossible to simulate the sound made by a snake, by shaking a rattle in the hand (Thwaites, 1896-1901, vol. 43, p. 153).

Other misunderstandings resulted from the names applied to the organ. For the rattle or rattle lobes, the earliest accounts used the Spanish *cascabel* (Cieça, 1554) and the Portuguese term *cascavel* (Magalhães de Gandavo, 1576, fol. 24r) meaning "a small bell"; so it is not strange that an early English report (Purchas, 1614, p. 842) should refer to the snake "which hath a bell in his tayle," or that one of the first Latin descriptions (Piso, 1648, p. 41) should use the term *tintinnabuli*, meaning bells. Thus we have several early reports likening the sound of the rattle to that of bells or cymbals (Marcgravius, 1648, p. 240; Jonstonus, 1653, p. 26; 1657, p. 23; Michel, 1916, p. 39, but written in 1703). Such terms are not at all appropriate. Neither are the references to continuous clicking sounds (Bonnecamps, 1920, p. 403, but written in 1749; Thwaites, 1896-1901, vol. 69, p. 167; Walsh, 1913, p. 716).

Some descriptions liken the sound to a child's rattle (Budd, 1685, p. 35; Bossu, 1771, p. 363; Dobrizhoffer, 1822, vol. 2, p. 287, first published in 1784; Holm, 1834, p. 53, first published in 1702). If the children's rattles of those days were hollow, nonmetallic devices, containing sand or seeds, the simile is apt. Champlain in about 1602 (Biggar, 1932-36, plate 46) actually pictured a snake with what appears to be a child's rattle or bell on its tail.

<sup>7</sup> That is, dry and rasping, without hum, ring, or metallic overtones. It is not toneless in the sense of lacking a substantially constant frequency.

Other mechanical devices were mentioned, such as many spinning wheels heard at a distance (Kalm, 1752–53, p. 313), the released spring of a watch (Daudin, 1801–4, vol. 5, p. 299), the ticking of many watches (McKenney, 1846, p. 114), or an alarm clock (Gharpurey, 1935, p. 44). Hartwig (1873, p. 298) thought the rattle sounded like a knife being ground; and Lacépède (1788–89, vol. 2, p. 407; Kerr's translation, 1802, vol. 4, p. 261; Fleming, 1822, vol. 2, p. 293) like the rumpling of dry parchment. Bosc (1803, p. 552) said it could be imitated by rubbing two goose feathers together. Simcoe (1911, p. 196) referred to the sound as whizzing, Thompson (1924, p. 71) as whistling, and Kipling (1928, p. 18) as sizzling. Hopley (1882, p. 300) called the sound sibilant. O. W. Holmes in *Elsie Venner* (1861, vol. 1, p. 238) called the sound a "long loud stinging whirr." Boulenger (1914, p. 184) suggests a resemblance to running water. Several authors believe the sound to be similar to that of dried peas or beans shaken in the pod (Juan and Ulloa, 1758, vol. 1, p. 62; Hopley, 1882, p. 300; Kipling, 1928, p. 18; Gillespie, 1937, p. 132), or melon seeds shaken in a box (Galinée, 1669, 1903, p. 41; Kellogg, 1917, p. 190).

A number of writers liken the sound of the rattle to that of various insects referred to as cicadas, locusts, crickets, or grasshoppers (Megapolensis, 1644, p. 169, ed. of 1909; Paul de Jeune, 1657, in Kenton, 1927, vol. 2, p. 85; also in Thwaites, 1896–1901, vol. 43, p. 153; Charlevoix, 1761, vol. 1, p. 343; Beal, 1872, p. 310; Hinton, 1878, p. 339; Anon., 1894, p. 124). To anyone knowing the loose way in which such entomological names are employed, these beliefs are probably well justified. There are, for example, species of cicadas in southern California and Arizona whose strident buzz is so rattlesnake-like that they are quite deceiving to the rattlesnake expert, and presumably to the entomologist as well. Hinton (1878, p. 339) claimed that the cicada could be recognized by its shorter, more uneven rhythm, but this is not true of some that I have heard. Anon. (1947b, p. 8) suggested that they might be distinguished because the insect's buzz would cease as one drew near, whereas the rattler would get louder, but I have encountered cicadas that would persist until one almost touched them.

Several authors have likened the rattle to the buzzing of a large bee (Harris, 1821, p. 59; Fitch, 1903, p. 315). Bieber (1936, p. 292) tells of a military camp in 1847 alerted at night because a buzzing bumble bee was entangled in a buffalo robe. I have never heard a bee that compared with a cicada as a rattle imitator. Darwin (1873, p. 107) reported that the rattle sounded like the hiss of an African puff adder, only louder. Our loudest North American hissers, the bull or gopher snakes of the genus *Pituophis*, can readily be distinguished from the sound of the rattle because their hiss is intermittent. Beadle (1879, p. 133) thought the sounds somewhat alike.

Other sounds reported as being similar to the rattle of a rattlesnake are blowing through loose lips (Dugés, 1879, p. 3; Terron, 1921, p. 182), the wind in the trees, the hissing of a hard rain, or escaping steam (Surface, 1906, p. 191). To my mind, I should choose, as those having the best likeness, either a small steam jet or some species of cicada. Duncan (1945, p. 172) said that a rattle sounds like a locust when the snake is not seriously disturbed, but like a pressure cooker with the safety valve open when the snake is really angered. Many of the other comparisons are quite inappropriate. In any case, it should be remembered that

the sound of a rattle is essentially a hiss, and any noise that does not answer to this characterization is ill-chosen as a rattle substitute. The best human imitation can be made by hissing through the teeth with the lips parted.

Throughout this discussion of rattle similitude, I have treated the subject as if all rattlesnakes of all species and ages made the same sound. This is, of course, far from the fact; my remarks, and those that I have quoted, are appropriate only respecting adult rattlers of the larger species, and even these only when equipped with rattle strings of some 5 to 10 rattles. Species and size differences will be mentioned subsequently.

It is well known that many kinds of snakes, both harmless and venomous, vibrate their tails when angered or frightened. Occasionally, when the tail is shaken amid dry leaves, a fairly good approximation to the sound of a rattle may be attained. Reuss (1951, p. 144) says that one of the rat snakes (*Elaphe obsoleta quadrivittata*) can make a hornet-like humming noise with its vibrating tail.

Some Old World vipers, including the saw-scaled viper (*Echis carinatus*) and the sand viper (*Aspis vipera*), make rustling sounds by rubbing the lateral scales of two body loops together. We have the word of Mosauer (1934, p. 61), who had field experience with the reptiles of both the Saharan and the American deserts, that the sound produced is like the rattle of a rattlesnake. Rose (1950, p. 260) says the African egg-eating snake (*Dasypeltis scabra*) also makes a hissing sound by rubbing its coils together. It is interesting to note that these sounds, like the rattling of a rattlesnake, are warning reactions producing somewhat similar sounds, but using quite different mechanisms.

Garman (1882, p. 174) and Grinnell, Dixon, and Linsdale (1930, p. 326) have reported that the young of the northern burrowing owl (*Speotyto cunicularia hypugaea*) can make a noise so like a rattlesnake as to deceive an experienced naturalist. These owls live in prairie-dog towns that are also inhabited by rattlers, and the authors think this imitation may protect the owlets from enemies that fear the snakes. Linsdale and Tevis (1951, p. 235) observe that a California ground squirrel can chatter its teeth with a sound like that made by a rattler.

#### METHOD OF VIBRATION AND THE PRODUCTION OF SOUND

When a coiled snake is rattling, the rattle string is pointed almost vertically, although tipped slightly backward. At this angle—about  $10^\circ$  from the vertical—the rattle is in a position of balance, owing to the asymmetry of the lobes, as discussed later. By being in balance is meant that the string will have no tendency to tip in any direction. However, because of the asymmetry, it can tip much farther forward than back, and it is normally held at a slightly greater backward tilt than a position of perfect balance, thus avoiding the possibility of having the end fall forward. In this balanced position, it will deliver the maximum noise for a given expenditure of energy and with the least wear. The vibration is always transverse or lateral, at right angles to the center line of the tail and to the flat or side face of the rattle.

On several occasions I have watched the operation of a sounding rattle under the light of a variable-frequency neon stroboscope. Snakes with particularly long rattle strings were used. It was most interesting to see the previous assump-

tions concerning the nature of the vibration borne out in these visual tests. With the stroboscopic light regulated to a frequency just below that of the snake's tail, the waves could be clearly seen going out from the tail to the end of the rattle string. The amplitude increases as the wave moves outward, because of the cumulative looseness of the interlocks between segments. The wave is much like that which may be sent along a loose rope.

If the segments of a rattle are moved slowly, with a transverse motion similar to that seen under the stroboscopic light, the method whereby the sound is produced may be analyzed. Between each lobe of each segment, and the interlocking lobe of the segment within, a succession of contacts and separations is produced, especially on the deep groove surfaces (fig. 5:12). No doubt each pair clashes at a number of different points, so that several distinct sounds are produced, as the wave passes each lobe. The total number of sounds per cycle equals twice the number of effective segments multiplied by the contacts per segment. Assuming only one contact per side of each segment, 3 lobes per segment, and a 6-rattle string, at 50 cycles per second (an average number), we have 1,000 contacts per second. It is obvious that a frequency such as this will result in a hiss rather than discrete sounds. A young rattler with only two rattles makes about 100 contacts per second; the result is a much softer buzz than the hiss of an adult. Since the rattle is hollow, dry, and the material somewhat pliable, like heavy parchment, the sound is unmetallic, lacking musical quality.

In addition to the ordinary high-speed vibratory motion, the snake, while rattling, often waves the tail slowly from side to side.

There are several myths concerning the method of producing sound with the rattle. One, current in Kentucky, is that a rattle, when cut off from a snake's tail, if held in the hand will continue to vibrate for about three hours. Fountain (1901, p. 80) thought it necessary to deny that the rattle sound was merely the result of rubbing the rattle on the ground or grass. The relationship of this idea to the equally erroneous one that the rattle always sounds when the snake moves, is apparent.

There is no indication of species differences warranting the suggestion by Moore (1951, p. 229) that the rattle serves for species recognition. Differences in size, within a species, will cause greater differences in the sound produced than would be evidenced between snakes of the same size, but of different species. And besides, rattlers are deaf.

#### SPEED OF VIBRATION

Wrote John Clayton in 1688 (published in 1693, p. 126): "The Old [rattlesnakes] shake and shiver these Rattles with wonderful nimbleness when they are any ways disturbed." No one can watch a rattler's tail in action, without being similarly impressed, for the tail end, and the rattles as well, are blurred by the rapidity of their motion. Mitchell (1860, p. 3) referred to the "marvellously rapid action" of the rattles. Ingersoll (1884a, p. 400) thought the speed could only be approached in nature by the hummingbird's wings.

The first serious attempt to measure the speed of the rattle was made by Ott (1882, p. 514) by means of a revolving drum kymograph. He found the rate of vibration to be about 60 cycles per second. Feoktistow (1889, p. 4; 1893, p. 57;

Stejneger, 1895, p. 388) attempted to make similar measurements. He obtained a rate of 75 vibrations per minute for the tail and 110 for the rattle. I assume that *minute* should read *second*; but even so, the test seems to have been faulty, for it is difficult to understand how the tail and rattle could have different vibratory rates. In fact, watching the operation of a rattle under stroboscopic light discloses a synchronized motion of tail and rattle, as would be presumed from the nature of the muscular effort applied. Williams (1920, p. 15) made tests on a western diamondback (*C. atrox*) and secured average rates of 20 to 21.4 cycles, with a considerable variation in successive cycles. The pitch of the rattle sound was judged by musicians to be between C and C-sharp, or from 128 to 135 vibrations per second.\*

Over a period of some six years, 1935 to 1940, I made a number of tests on rattle speeds, and published the results in the latter year (1940b, p. 13). The following is an abridgment of that report:

To secure speed records, a simple kymograph, driven by a synchronous motor on a controlled-frequency circuit, was employed, with stylographic paper on the drum. For registration, a pin was run vertically through the proximal segment of the rattle, with the point inserted downward between the rattle shell and the flesh of the matrix. The snake was held with the neck in the left hand and the posterior part of the body in the right. The vibrating tail was then lowered until the pin touched the kymograph drum. As it was later found that the speed of vibration was characteristic of each snake, and its condition and disposition, rather than the weight of the rattle string, it is believed that the pin weight did not affect the result. Similarly, as the scratch on the waxed surface was usually so fine as to require a magnifier for its examination, the drag of the pin is not thought to have been a source of serious error.

Altogether, 173 records were made on 81 snakes of 20 different species and subspecies. It was found possible to get good records in most cases when large specimens not long in captivity were used. The juveniles of the large species, or adult snakes of the smaller forms, did not produce legible records. Specimens long in captivity seldom reacted efficiently; and even fresh specimens often refused to rattle properly, after being held for a few moments, in spite of being vigorously pinched.

Although I suspect that there may be some specific differences in rattle speed—the longer-tailed forms, such as the Central American rattler (*C. d. durissus*), vibrating their tails at a slower rate than the southern Pacific rattler (*C. v. helleri*), for example—I soon gave up any hope of proving this statistically, for various other conditions, such as the temperature and the degree of anger or fear evidenced by the snake, produce such wide variations as to mask completely any species differences.

The kymograph records indicate that, for each snake, under specific conditions, the rattle attains full or characteristic speed within a few cycles—there is no gradual coming up to speed. The same conclusion was reached from observation of snakes making the spasmodic or nervous clicks with which they often begin or end a sound of the rattle; these are really short runs of the rattle at full speed.

\* The difference between rattle rate and the tone is to be accounted for by the number of lobe impacts per cycle. The rattle rate is so low that the accuracy of the method may be questioned.

However, there are occasional variations within short ranges. For example, a specimen of the Panamint rattler (*C. m. stephensi*) changed from a speed of 54 cycles per second to 45 within two cycles.

The tail vibration seems closely to follow simple harmonic motion. To amplify the kymograph record, a needle was run longitudinally down the center of the long rattle string of a large snake, thus making it a rigid, but light, extension of the tail. The end of the needle was allowed to touch the kymograph drum and the resultant curves were photographically enlarged. The wave was analyzed and found to be almost a pure sine wave, the third and fifth harmonics having an amplitude of only about 3 per cent of the fundamental, and the higher harmonics 1 per cent or less.

I have stated that the wave, as seen under stroboscopic light, gains in amplitude as it travels out toward the end of the rattle, because of the cumulative looseness of articulation between segments. At the matrix itself the amplitude is quite small—hardly more than a millimeter or so on each side of the center line—even in a large snake. A young eastern diamondback (*C. adamanteus*) 830 mm. long, vibrating its tail at the rate of 51 cycles per second, had an unusually large amplitude; this was measured and found to be 3.4 mm. from right to left peak, or a motion of about 1.7 mm. on each side of the center line. This is certainly greater than the average motion, which, in a snake a meter or so long, is found seldom to exceed 2 mm. between extremes, and is usually between 1 mm. and 1½ mm. But the rattle itself, particularly at the outer end, has a far greater motion because of its looseness. A study of kymograph records indicates that under constant temperature conditions, if there be a change in speed there is likely to be a change in amplitude as well; a lower frequency accompanies a lower amplitude.

An elementary test is sufficient to prove the important effect of temperature on the speed of vibration. Eight runs on 5 specimens of prairie rattlesnakes (*C. v. viridis*) from South Dakota at a temperature of 11° C. (51.8° F.) produced an average rattle speed of 41.0 cycles per second (max. 44.9, min. 28.1); in ten tests on six specimens at 23° C. (73.4° F.) the average speed was 57.9 cycles (max. 66.9, min. 53.2). Thus an increase of 12° C. (21.6° F.) raised the speed about 41 per cent. The weight of the rattle has virtually no effect on the speed, as shown by several tests in which segments were successively removed from the strings.

There seems to be no appreciable sexual dimorphism; nor was I able to find any consistent trend of rattle speed with size. At temperatures of from 18° to 24° C. (64.4° to 75.2° F.), with the subspecies tested, which included *C. d. durissus*, *C. b. basiliscus*, *C. e. enyo*, *C. m. molossus*, *C. atrox*, *C. r. lucasensis*, *C. r. ruber*, *C. exsul*, *C. v. viridis*, *C. v. abyssus*, *C. v. lutosus*, *C. v. oreganus*, *C. v. helleri*, *C. m. pyrrhus*, *C. m. stephensi*, *C. l. lepidus*, and *C. l. klauberi*, it was seldom that the speed was above 60 or below 40 cycles per second, with an average of about 48 cycles. The lowest speed recorded was 28.1 cycles at 11° C. (51.8° F.), and the highest 66.9 at 23° C. (73.4° F.), both in the prairie rattler (*C. v. viridis*). No tests were made at temperatures above 25½° C. (77.9° F.).

To determine the amount of fluctuation in speed in a continuous sounding of the rattle, I measured the lengths of successive cycles and secured the following: Total cycles 147; mean speed 46.09, maximum 52.6, minimum 41.7, inter-

quartile range 44.67 to 47.64 cycles per second; coefficient of variation 4.82 per cent. Probably the true variations are somewhat less than these figures since the method of measurement tends to exaggerate the fluctuations. This test was made on a prairie rattler at 23° C. (73.4° F.).

I found nothing to justify the suggestion of Hopley (1882, p. 312) that a snake changes the speed of the rattle deliberately to vary its signals. Besides the important effect of temperature, the fact that a higher amplitude accompanies a higher speed indicates that a greater degree of alarm or anger tends to accelerate the rattle. These seem to be the most important factors affecting the vibratory rate under constant temperaure conditions.

Subsequent to these tests, I made an additional endeavor to secure speed records from juveniles, using a calibrated neon stroboscope, but with indifferent results, as the young snakes would not rattle continuously enough to produce satisfactory readings. One 2-rattle western diamond (*C. atrox*) rattled at the rate of 56.9 cycles per second at a temperature of 25° C. (77° F.). Four adults of the same species, under the same conditions, ranged from 48.0 to 51.8 cycles, with an average of 50.2 cycles. Thus, this single series of tests indicated a higher vibratory rate in the young specimen, but this requires further verification. Two northern Pacifics (*C. v. oreganus*) had rates of 47.4 and 50.7 cycles, the first having a long and the other a short string. A single sidewinder (*C. c. laterorepens*) had the low vibratory rate of 34.9 cycles.

The most complete and accurate study of the variations of rattle speeds at different temperatures were those lately reported by Chadwick and Rahn (1954, p. 442). Rattle speeds were determined by a mercury-arc stroboscope, and temperatures by a mercury thermometer introduced via the cloacal opening. The snakes tested were 16 freshly captured adult prairie rattlesnakes (*C. v. viridis*) from Wyoming. Altogether, 226 observations were made at temperatures varying from 8° C. (46.4° F.) to 36° C. (96.8° F.). Both the scatter plots and the group averages indicated a linear relationship represented by the equation  $R = 155\ T - 283$ , where  $R$  is rattle speed in cycles per minute and  $T$  the temperature in degrees centigrade. Transforming this into cycles per second, to conform to the units previously used in this discussion, we have  $R = 2.583\ T - 4.717$ . This gives the following approximate speeds at various temperatures:

Degrees Centigrade	Degrees Fahrenheit	Cycles per second
10	50	21.1
15	59	34.0
20	68	47.0
25	77	59.9
30	86	72.8
35	95	85.7
40	104	98.6

It will be noted that the gain in speed is about 2.6 cycles for each degree centigrade rise in temperature, or somewhat less than 1.5 cycles for each degree Fahrenheit.

## FORMATION AND STRUCTURE

## CHRONOLOGY OF RATTLE FORMATION

Much has been written about the chronology of rattle formation, and the relationship between the number of segments in the rattle and the snake's age. The rattle-per-year idea was first put in print by Hernández (1615, fol. 192r; 1628 and 1651, p. 328) and is still widely believed. No snake myth was ever more indelibly imbedded in the public consciousness, as may be seen by frequent newspaper reports down to the present day. And it is small wonder, for the great majority of the early accounts of the rattlesnake reiterated this entertaining myth, and there is something peculiarly satisfying in having so concrete a record of a creature's age. So we find it repeated by Vázquez de Espinosa (1629; ed. 1948, p. 197), Nieremberg (1635, p. 269), Morton (1637, p. 82), Piso (1648, p. 41), Marcgravius (1648, p. 240), Jonstonus (1653, p. 26; 1657, p. 23), Van der Donck (1655; ed. 1909, p. 298), Nieuhof (1682; ed. 1704, vol. 2, p. 15), Clayton (1693, p. 126), Holm (1702; ed. 1834, p. 53), Charlevoix (1761, vol. 1, p. 343), Bossu (1771, p. 364), LePage du Pratz (1774, p. 269), Carver (1778, p. 480), Zeisberger (1779; 1910, p. 70), Dobrizhoffer (1784; 1802, vol. 2, p. 287), Pennant (1787, p. 87), Anburey (1789, p. 387), and Bosc (1803, p. 553). Later reaffirmations are too numerous to mention, but it is worth noting that the theory was reiterated in the very influential *Illustrated Natural History* of Rev. John G. Wood (1863, vol. 3, p. 100) and its innumerable subsequent editions, although it did not appear in the first edition (1851-53) or those that immediately followed, until the enlargement of this popular work in 1863.

Denials of the age-from-the-rattle theory were not slow in coming, though they have never caught up with the myth and never will. The earliest disavowals emanated from two supposedly controverting facts, one of which depended in itself on another myth, the other on a discrepancy that is valid. To some it appeared impossible that a snake could be as old as indicated by reputed rattle strings of 40 to 80 segments; to others it was evident that rattles were subject to breakage and therefore could not invariably give the correct age. Grew (1681, p. 51), who was probably the first to question the age-from-the-rattles theory, had seen a 16-rattle string and thought it very doubtful that rattlers could live so long (actually, some do attain this age). Catesby (1743, vol. 2, p. 42) doubted the myth because he had found small rattlesnakes with more segments than large snakes. Lacépède (1788-89, vol. 2, p. 407; Kerr's translation, 1802, vol. 4, p. 260) stated that breakage would interfere with the age determination, even if the snakes did get a rattle a year. His criticism was, of course, the most pertinent of all; up to that time it seems not to have been realized how seldom adult rattlesnakes have unbroken strings.

Shortly after this, observations of captive snakes showed that snakes could, and often did, acquire more than a rattle a year (Barton, 1800, p. 39; Ord, 1815, p. 358; Say, 1819, p. 262). From this time on, the more scientific treatises no longer advanced the age-from-the-rattle theory, although the related rattle-a-year belief was more persistent.

As early as 1790, Lacépède (vol. 2, p. 405; Kerr's translation, 1802, vol. 4, p. 258) had reached the conclusion, from the rattle structure and its method of formation, that the acquisition of each new rattle must be coincident with shedding; however, he was not sure that the shedding of the skin of the snake's body was coincident with the shedding of the skin of the tail. The theory of the coincidence of shedding with the formation of the new rattle received additional emphasis from Schlegel (1837, vol. 2, p. 557) and Garman (1893, p. 102) without the qualification respecting the noncoincidence of the shedding of the body and tail. The hypothesis is obviously related to that theory of the genesis of the rattle which visualizes a gradual modification of the shape of the terminal cone on the tail, whereby successive sheddings of this spur would be interlocked and retained. While there has been a gradual acceptance of this belief of the coincidence of rattle acquisitions with shedding, fully confirmed by the recent important histological researches of Zimmermann and Pope (1948, p. 353), yet there have been those who have reported contrary conclusions, some of which were based on experiments (Brown, 1881b, p. 106; Hopley, 1882, p. 298; Lugger, 1883, p. 266; Feoktistow, 1889, p. 1; 1893, p. 54; Gibbs, 1892, p. 7; Stejneger, 1895, p. 384; Lydekker, 1896, p. 239; Storer and Wilson, 1932, p. 169; Curran and Kauffeld, 1937, p. 50; Breland, 1948, p. 199). Of these dissenters, the most important was Feoktistow, whose observations and conclusions were given wide circulation in textbooks and natural histories, so that they are still affecting the acceptance of the coincidence theory.

Yet, as I reread Feoktistow and the others who performed original experiments, I cannot but be impressed by their seeming lack of appreciation of some of the irregularities that affect captive rattlesnakes, especially those that are given imperfect care, or that have never become accustomed to captivity and refuse to eat. In such circumstances we see them sluggish, a prey to starvation and disease, their skins shed at irregular intervals, and often in strings and patches, rather than entire as in a normal snake. Small wonder then, that the observer is unable to note whether a fresh segment is disclosed coincident with each shedding, or whether the total segments acquired in a given period equal the number of moults in the same time. Sometimes the posterior end of the old skin may pull away from the previous rattle and disclose the new segment several days before the skin is shed. Under such circumstances, unless the rattles are carefully counted, an addition will not be noted as accompanying the skin change. Also, it is possible that a segment may be lost at about the time the new rattle is disclosed, and this will not be observed unless each segment be appropriately marked or numbered. But when the snake is healthy, the shedding normal, and the rattles so marked that a new lobe is easily recognized, then complete coincidence between skin-shedding and rattle acquisitions will be observed, as would be expected from the homology between the skin and rattle, as discussed elsewhere (p. 302).

If we agree that rattlers attain a new rattle each time they shed, we still have not established the chronology of rattle development—we have merely related it to that of shedding. This shedding chronology has been adequately treated in another chapter (p. 359), wherein the conclusions were reached that young rattlers in the wild shed 3 to 4 times in each of their first two years, after which, as adults, they shed from about 3 times per year, where the climate permits almost

year-round activity, to little more often than once per annum, where their activity is limited to about 6 months of the year or slightly less. Among captive rattlers, especially those kept in cages that are warmed in the winter, skin shedding is more frequent, reaching as many as 6 or 7 per year in the young, and 3 or more among adults.

Some rather queer variations of the shedding theory have been proposed, such as that of Barnes (1928, p. 396) to the effect that one or two rattles come off with each shedding of the skin; and that of Cook (1943, p. 51) that the sheddings and rattle acquisitions are coincident up to maturity, after which no new segments are formed. One queer myth has it that a rattlesnake gets a complete new string of rattles each year, as a deer gets a new set of antlers, and that each new string is one segment longer than the old (Koenig, 1906, p. 49). Another theory recently overheard at the San Diego Zoo is that each year, while a snake is in hibernation, it acquires a new rattle at the *outer end* of the string, each button, in turn, becoming a larger and more mature rattle.

Regarding the chronology of the rattle, there were, and still are, some special myths affecting only young rattlers, which in turn modify the age-from-the-rattle theory. One school of thought adhered to the belief that a rattler has no rattles until it is from 1 to 3 (usually 2) years old. This completely erroneous idea was apparently started by Clayton (1693, p. 126), who must have misidentified some other snake—he said he knew it was a rattler from the pattern, although it had no rattles. The belief was subsequently reiterated by Brickell (1737, p. 144), Salmon (1744–46, vol. 3, p. 413), Brookes (1763, vol. 3, p. 370), Goldsmith (1774, vol. 7, p. 209), Anon. (1815, p. 152), Ferrall (1832, p. 300), Buckingham (1842, vol. 2, p. 178), Bigland (1844, p. 136), Anon. (1872b, p. 642), Meline (1873, p. 45), Bailey (1876, p. 404), Lugger (1883, p. 266), “Camerambler” (1900, p. 384), Brehm quoted by Koenig (1906, p. 49), Rutledge (1921b, p. 218), and Unonius (1950, vol. 1, p. 297, but writing in 1841–58). Walsh (1913, p. 716) mentions the theory as a popular belief to which he himself did not adhere. As recently as 1949, Pinkerton (p. 19) was asked by a correspondent whether it was true that a rattler got its first rattle at the age of 5 years.

I know of no better example of how a single inaccurate observation can become so widespread through repetition as this of Clayton’s. Of course, there are two other misunderstandings that may have served to perpetuate this peculiar myth, the first being a failure to identify the button as a rattle; and the second resulting from a confusion of terms, the rattle only being recognized as such when it includes at least one loose segment and thus becomes audible. This—the acquisition of rattle No. 2—may not occur for as much as 6 months or more after the birth of the young snake, the interval varying with the ability of the young snake to secure food, and the length of its first hibernation.

Another myth (of which I was informed by K. P. Schmidt), resulting from misidentifications, reports that young rattlers often throw off their rattles when they first use them, which accounts for the snakes with sharp tails that are really rattlers but are thus disguised. The fact that rattlesnakes without rattles are occasionally found is not an argument in favor of this theory of the delayed acquisition on the part of the young, for such freaks are adults suffering from some accident or congenital defect. Usually it can be judged from scars on the anomalous snake

that the rattler was thought to have been killed and its rattles—together with the rattle-forming matrix—were cut off by someone desiring them as trophies, after which the snake recovered. No less than 5 mutilated in this way were contained in the Platteville series of some 800 prairie rattlers (*C. v. viridis*).

Here is another way in which rattleless rattlers may occur:

While fighting a Salmon River grass fire, several years ago, two rattlesnakes were encountered. Both had their rattles burned off. They were in a bad frame of mind and made repeated attempts to come in to close quarters and bite. As they could give no warning rattle, they were particularly dangerous. *Howard W. Higgins, U. S. Forest Service, Avery, Idaho.*

Hopley (1882, p. 298) shows a sketch of the defective rattle of a snake sent to the London zoo. This was a sort of cone that was neither added to nor dropped with successive sheddings. I have seen a Uracoan rattler (*C. d. uegrandis*) with a defective matrix that produced a succession of 10 segments, all of which, except the button, were of the same size. The button, although slightly smaller than the succeeding rattles, was abnormally large for this subspecies. Sass (1935, p. 627) thought that the myth of the horn snake (the creature with the tree-killing sting in its tail) may have arisen from the case of a rattler, whose rattle, for some reason, had become solidified into a single long point.

I have seen in the wild only one rattler with a defective tail that was sharp enough not to show clear evidences of having been despoiled of its rattles by a trophy hunter. This was an adult Mojave Desert sidewinder (*C. c. cerastes*) taken alive by Charles E. Shaw and myself 11 miles north of Shoshone, Inyo County, California, on June 4, 1949. As shown in the photograph (fig. 5:15) the tail is pointed, with no vestige of a rattle. Whether this freak resulted from an accident or a congenital defect, I cannot say; it was probably the latter. Subsequently it gave birth to normal young.

Among preserved rattlesnakes, I have seen three without rattle strings, evidently caused by congenital defects rather than the results of accident or trophy hunters. One was a timber rattler (*C. h. horridus*) from Iowa with a single, small, pointed rattle. Evidently the matrix was defective in form, so that successive segments would slough away when the skin was shed, having nothing to grip in the succeeding lobe. The second was a twin-spotted rattler (*C. p. pricei*) with a tail coming to a moderately sharp point and without a vestige of a rattle. The tail was shorter and with fewer than normal subcaudal scales. No scar was evident, so it is probable that the defect had been present from birth. The third was the holotype of *C. catalinensis*, of which the tail end was covered with a single ungrooved segment to which no prior rattle might cling.

It is my hope that mention of these few rattleless rattlesnakes will not increase the frequency with which sharp-tailed snakes are misidentified as rattlesnakes, because of some fancied likeness. From my experience, I should judge that defects of this congenital type occur in about one rattlesnake in five thousand.

Equally fantastic, and just as persistent as the theory that rattlesnakes acquire no rattles until they are several years old, has been the belief that rattlesnakes are occasionally born possessed of 2 or 3 rattles. This idea was first voiced by Barton (1800, p. 39), was repeated by Mease (1807, p. 391) and Hopley (1882, p. 299), and has been revived quite recently (Curran, 1935, p. 332; Curran and

Kauffeld, 1937, p. 50; Devoe, 1945, p. 484; 1951, p. 226). Even Stejneger (1895, p. 383) thought it possible that a rattler might shed before birth; however, even this would produce only the button, so that 2 sheddings before birth would be necessary if a young rattler were to be born with 2 rattles.

Reading Barton's original account leaves no doubt that this story emanated from an error in dissection. He tells us that he removed the embryos from several females when the young were about the thickness of a small goose quill and some 5 inches long. The rattlesnakes available to Barton were timber rattlers (*C. h. horridus*), the young of which at birth are normally about 285 mm. (11¼ in.) long and 10 mm. (¾ in.) in diameter. One may note how tiny and immature were the embryos that Barton examined; yet, of these, he found no less than 60 to be possessed of 3 rattles. That he misinterpreted some conformation in the tails cannot be questioned. Like Clayton's story of the rattleless young, the long-lived myth of the surplus rattles at birth was based upon a phantom foundation.

I know of no other report of 2 or more rattles at birth. Nothing of the kind has been seen among the hundreds of embryos and freshly born snakes that I have examined. Even Lombard's claim (1881, p. 88) that a rattler has 3 rattles within 6 weeks of birth is an exaggeration, since young rattlers do not usually acquire their second rattles until at least 2 months after birth; and in the majority of instances this is delayed until after the first hibernation. In one series comprising 139 young western diamond rattlers (*C. atrox*), born in late August and preserved a month later, 3 specimens had acquired their second rattles. In the Platteville series of prairie rattlesnakes (*C. v. viridis*) collected while entering or leaving hibernation, out of 226 young-of-the-year (after about 2½ months of active life), 44 or 19½ per cent, had already achieved a second rattle, and one had 3, although there may be some question whether this individual was not a stunted snake belonging to the previous year's crop.

Rose (1929, p. 222) tells a yarn—to which he does not subscribe—of a collector who gathered rattlesnake eggs, and claimed to hear the young rattling in their shells before they hatched, a story rendered somewhat doubtful by reason of the fact that rattlesnakes do not lay eggs but give birth to living young.

Upon the acceptance of the theory of the coincidence of shedding with the acquisition, or at least the disclosure, of a new rattle, one seemingly inexplicable and discordant feature appeared, namely, the fact that, after their first shedding, young rattlesnakes still possessed only one rattle, when they should have had two, one to match the original skin with which they were born, and the second, the newly acquired skin. This problem was solved by the present writer in 1940 (1940b, p. 25), upon observing that the rattle with which a snake is born, and to which the term prebutton was applied, is invariably shed with the first skin. Garman (1888, p. 260; 1889, p. 174; Stejneger 1895, p. 382) had noted the difference in shape between the prebutton (fig. 5:3), and the true button, or first permanent rattle (fig. 5:4), but thought the one was transformed into the other by a stretching, accompanied by a constriction at the outer end and a swelling of the proximal edge, thus acquiring the characteristic shape of the button.

This is found to be contrary to what actually occurs; for, from observations of live specimens of recently born broods, it is found that when the birth-skin is shed the prebutton goes with it. This loss occurs for two reasons: first, the thinness and

fragility of the prebutton; and, secondly, because its configuration, and that of the true button beneath, are such that it cannot retain a grip on the latter. The crimped edge of the prebutton is too pliable and weak to prevent opening, and furthermore, the central transverse groove in the button is too shallow, so that there is little for the prebutton to grip. As a result, the prebutton is shed just as the skin itself is lost. Usually it is shed as a part of the skin; in fact, the prebutton is hardly distinguishable from the skin except upon close examination. Its very softness may cause it to be overlooked in the shed skin of the baby rattler; and it is hidden by the inside-out skin of the tail. In this shedding we discern the homology between the skin and rattle.

The fact that baby rattlers shed shortly after birth is verified by observations on broods born in captivity; this is a schedule characteristic of most snakes, whether oviparous or ovoviviparous. Among rattlesnakes, the interval between birth and shedding has been found to be 7 to 10 days, ordinarily. Some example records have been presented elsewhere (p. 731).

The early European herpetologists were handicapped by the lack of adequate material wherewith to determine how the rattle is formed and the relationship between successive segments. Lacépède (1788–89, vol. 2, p. 396; Kerr's translation, 1802, vol. 4, p. 252) described the method of formation with considerable accuracy; he also noted the change in rattle size as a snake grew, and the resulting taper in the rattles of adolescent snakes (p. 407; Kerr, p. 259); however, he did not recognize the peculiar character of the button. This was noted by Bosc (1803, p. 552), who, for the first time, was able to point out the criteria upon which one might decide whether any given string was or was not complete.

#### RATTLE-STRING LENGTH

"James Morton yesterday killed a big rattlesnake on the bank of Trout Creek. It measured nearly 5 feet and had 16 rattles and a button." *Blank County Weekly Herald*.

So reads a typical newspaper report, and from it the skeptic will conclude that, regardless of the snake's actual length—no doubt nearer 3 than 5 feet—the chances of its really having had 16 rattles and a button were remote, indeed. For the statement implies the coincidence of two rare events: a rattle string on a wild<sup>o</sup> rattlesnake containing as many as 16 rattles; and, superimposed on this, the still greater improbability that the string was unbroken, not a single segment having been lost since the first shedding, for this is what the retention of the button means. Citing the presence of a large number of rattles seems, to the average person, a proof that the snake must have been truly a monster; but actually these long strings are so unusual that the herpetologist immediately doubts all the details of any story of which a long string is a part.

Besides plain lying, or, in milder terms, exaggeration, there are several ways in which these long strings become established beliefs. Sometimes there is a miscount. Then there are faked rattle strings, obviously not to be expected on wild snakes unless a rather intricate practical joke is involved, although often attached to skins that serve as ornaments or trophies. Again, many people count,

<sup>o</sup> In discussing rattlers, the term *wild* is used, not in contrast with *tame*, but to distinguish the snakes as found in the wild, from captive specimens, especially those long in captivity.

as an additional rattle, each lobe of the terminal segment of a broken string, which adds at least 2, or occasionally 3, to the count. Sometimes the counter estimates the number of rattles that have been lost from an incomplete string and includes these departed wraiths, on the theory that the snake has played unfairly in losing them. Some people double the number by counting each side of the central crease. But mostly the long strings are just hearsay, the persistent echo of some campfire tale.

There were several long-string stories that became classics in their day; indeed, one of them still persists. The first was that of Dudley (1723, p. 294), who published a report of the killing of a rattlesnake having a string of between 70 and 80 rattles. Since this yarn appeared in the sedate *Philosophical Transactions* of the Royal Society (London), it was occasionally accepted (e.g., Pennant, 1787, p. 87), but it probably was not taken seriously by many, since who could conceive of a rattler 70 to 80 years old? Besides, the venerable creature not only had these proofs of a great age, but a sprinkling of gray hairs as well—a logical but last-straw addition, too much for even the most credulous. Hunter's report (1823, p. 178) of a rattler on the Upper Missouri with 90 rattles seems never to have gained credence, nor did the monster, quoted by Goode (1874b, p. 123) from a newspaper report, which not only had 87 rattles, but weighed 117 pounds. Two long strings, cited by those who mention them as being frankly in the folklore class, were a string of 75 rattles on an 18-foot diamondback in Florida (Robinson, 1896, p. 711); and a 100-rattle string on a 12-foot prairie rattler (Vestal, 1941, p. 146).

A much longer-lived phenomenon was a 44-rattle string, first reported (and pictured) in the *Columbian Magazine or Monthly Miscellany*, of November, 1786, pp. 107–8. The article is by that bashful author, Anon. Although purporting to discuss the habits of the timber rattlesnake (*C. h. horridus*), the account is largely dedicated to this extraordinary rattle, said to have been found on a snake killed during the previous summer at Fort Allen. The figure (see fig. 17:7, this book) is well drawn and apparently, as stated, full-size, the length of the rattle string being  $6\frac{3}{4}$  inches (175 mm.). The engraving is sufficiently detailed to show clearly that this is a faked string comprising 7, or possibly 8, separate sections. It is an incomplete string of 42 segments, with a terminal 3-lobe rattle, hence the "44 rattles." This ancient counterfeit has been mentioned in the literature many times, both as a maximum record of string length and of rattlesnake age, one of the most recent citations being that of Berridge (1935, p. 62).

Other long strings pictured in such a way that the discontinuities can be detected, include the 42 rattles-and-a-button of Anon. (1903b) comprising about 7 sections, and Catesby's figure of a *C. horridus* (1743, vol. 2, plate 41) with 23 rattles (labeled as having 24), apparently made up of at least 2 sections, one of 15 and the other of 8 rattles (fig. 17:5).

Several extra-long strings have been pictured that can be seen to be fictitious, not through the evidence of unmatched sections, but by reason of their shapes. These show a series of rattles gradually increasing in size from the original button to the latest rattle joining the string to the tail, that is, with a uniform taper throughout. Actually, rattles do not follow any such growth sequence, for

there is little or no growth in lobe size after the acquisition of about the tenth or twelfth rattle. In other words, were there an authentic complete rattle string of some 40 segments, the terminal 10 or 12 would taper almost to a point, but the remaining 30 would be substantially equal in size. Thus, we know the imaginary character of some of the early strings from their pictures. In this category fall the string of 41 shown by Seba (1735, vol. 2, plate 96) and the additional strings of 36, 31, and 19 in his plate 95 (fig. 17:4, this book). Houttuyn's 41-rattle string (vol. 16, plate 54, figure 1, 1764) is probably a repetition of Seba. Then there is the string of 44 rattles on a "wood" rattlesnake depicted by Shaw (1802, pt. 2, p. 335), clearly of this impossible shape (fig. 17:8, this book). Much more recent was the 42-rattles-and-a-button string pictured by the late Believe-It-or-Not-Ripley (*Los Angeles Examiner*, Nov. 7, 1947), which was of the same implausible character, although with a less continuous taper than those of Seba and Shaw.

Omitting such indefinite statements as those of Winterbotham (1795, p. 405), respecting the occurrence of strings of 40 to 70, Rees's (1819, p. [1]) mention of 40 to 50, and Reid's (1889, p. 226) of a rattle string about one foot long, which would indicate about 70 rattles, we have a number of additional reports of specific long strings. They follow in a declining order: 52 Lloyd (1951, p. 30); 36 Mitchell (1868, p. 453), Spielman (1950, p. 29); 33 Dorsch (1929, p. 3); 32 Weld (1800, p. 409), Tixier (1844, p. 76, ed. of 1940), Ingersoll (1884a, p. 400; 1884b, p. 97), Ellsworth (1918, p. 433)<sup>10</sup>; 30 Brickell (1737, p. 144); 29 Anon. (1815, p. 152), Dexter (1884, p. 124); 28 Chalmers (1878, p. 422); 27 Herrick (1953, p. 23); 26 Goode (1874b, p. 123), Menger (1905; 1913, p. 136); 25 Dumont (1753, vol. 1, p. 109), Hopley (1882, p. 301); 24 Maude (1828, p. 150), Walduck in Masterson (1938, p. 214); 23 Sass (1935, p. 251), Messeling (1953, p. 23); 22 Goode (1874b, p. 123), "Loch Laddie" (1908, p. 979), Grinnell and Storer (1924, p. 647), Sass (1935, p. 251); 21 Holbrook (1838, vol. 2, p. 85; 1842, vol. 3, p. 15), Ingersoll (1884a, p. 400; 1884b, p. 97), Mivart (1888, p. 293), "Juvenal" (1900, p. 24), Gharpurey (1935, p. 154); 20 Mather (1714, p. 67), Ker (1816, p. 20), Meline (1873, p. 276). Below 20 the reports are too numerous to be worth recording, even though they are probably more credible than those involving the higher numbers.

Of course, at this late date, it is impossible to determine which, if any, of these strings may be accepted as authentic. Only one was represented by a photograph; this was the 26-rattle string reported by Menger, clearly a faked string comprising 4 sections. I have no doubt that many of the others are based on fabricated strings, not perpetrated by the authors, but by those who claimed to have caught or killed the rattlers involved. In this same category we may place a string of 44 rattles exhibited for many years in a Texas drug store. The fact that the rattles were said to have been found on a snake 12 feet in length casts added doubt on their genuineness.

Phenomenally long strings are often cited as proof that their possessors were of phenomenally large size, although, in reality, this proof only throws additional doubt on the entire story, and the same conclusion is sure to be drawn from a multiplicity of long strings. Hence we must infer exaggeration when we learn that Messeling (1953, p. 23) on Plum Creek, in southwestern Wisconsin, killed

<sup>10</sup> He also mentions a string of 52 that he concedes was faked.

one lot of timber rattlers (*C. h. horridus*), every one of which had a string of from 16 to 19 rattles. A single rattler with such a string would be deservedly worthy of remark.

The faking of rattle strings is comparatively easy, and quite deceptive results may be attained if one has an adequate stock of separate short strings from which to choose well-matched sections when piecing them together. For it is not only necessary to make the successive sections match in transverse width, but in the other dimensions and in color as well. Some rattles, even when from snakes of the same size and subspecies, are more compressed longitudinally than others. All of these differences must be avoided if the section boundaries are not to be evident. Before joining the sections they should be softened by moistening, after which they can be telescoped into each other without breakage. While the reverse process of separating successive rings is said by Rivers (1874, p. 507) and Hopley (1882, p. 297) to be easy, actually the interlock is such that separation cannot be effected without breakage unless the rattles be softened and parted with the greatest care. Some prefer milk for softening.

Ditmars (1907, p. 432; Verrill, 1937, p. 31) says that in some snake exhibitions, long strings are faked to improve the appearance of the snakes displayed, but usually faking has the purpose of convincing the unwary of the truth of a fantastic story of the size and age of some rattlesnake reputed to have been killed in the wild.

Many of these long-string records in the literature are premised on hearsay rather than on personal observation, as the writers themselves make clear (e.g., Lloyd, 1951, p. 30). Some undoubtedly refer to captive specimens, which not infrequently attain long strings while secluded and inactive in their cages. Knowing the rarity of long strings and the prevalence of drawing the long bow with regard to rattlers, I should doubt whether more than 3 or 4, out of all those cited in the list, were authentic strings of wild rattlers. Of the many thousands of rattlers that have been brought to the San Diego Zoo in the past 25 years, none has had more than 16 segments in its rattle. This record string was on a Colorado Desert sidewinder (*C. c. laterorepens*), a sand-inhabiting form characterized by long strings. None of my correspondents has reported any phenomenal string on a rattler caught by himself in the wild. Of two collectors of particularly wide experience, one reported a 16-rattle maximum, the other 13. Another collector had seen a string of 32 rattles reputed to have been found on a Mojave Desert snake. My informant did not say how closely he examined the rattles to detect a possible fabrication.

The longest apparently authentic string I have ever seen was kindly sent me for examination by Stanley Mulaik of Salt Lake City. It was a string that had been removed from a western diamond (*C. atrox*) killed by a boy in the vicinity of Edinburg, Texas. It had comprised 23 segments, at one time, although when I saw it there were 19. The segments were unusually large, which would have made them hard to match. Neither C. B. Perkins nor I could detect any evidence of fabrication, Mr. Mulaik having forwarded the rattle to see whether it appeared to us to be genuine.

Skeptics of the authenticity of these long strings have not been lacking since early days. Kalm (1752-53, p. 315) wrote that he had been informed of strings

of 40, 30, and several of 20, but he had rarely seen one exceeding 12. Flack (1866, p. 316) said he had heard campfire tales in Texas of huge snakes with 30 rattles, but he thought that actually 12 was to be considered a high number.

Some early theories visualized an upper limit to the number of rattles, not owing to breakage, but to some natural limitation. Thus Loskiel (1794, p. 87; Anon., 1932b, p. 99) believed that a snake acquired a rattle a year until a limit of about 20 was attained. Stockbridge (1843, p. 41) thought there was some form of restriction affecting particular species—pigmy rattlers acquiring only 3 to 7 rattles. Holley (1836, p. 104) thought this species had no more than 2 rattles and a button. There is no validity to these supposed types of limitation.

Some authors record an old Indian myth to the effect that the number of rattles on a snake represents the number of its victims (I. Holmes, 1823, p. 258; Wood, 1863, vol. 3, p. 101). O. W. Holmes referred to this myth in his novel *Elsie Venner*. Tennent (1860, vol. 1, p. 194) mentions an item of Singhalese folklore in reverse; whenever a cobra expends its venom by biting, it loses a joint of its tail.

Although rattle strings of record length are of unquestioned interest, they are so rare as to be of little importance as factors in rattlesnake life and activity. These long strings, if they did exist, would be quite inefficient for their intended purpose—namely, to make a noise. We shall therefore present some data on the usual lengths of rattle strings on wild rattlers, and the reasons for the scarcity of long strings; for they are not scarce because rattlers do not grow so many segments during their lives—from this viewpoint 25 or 30 would not be exceptional—but because long strings are particularly subject to wear and breakage.

In gathering pertinent data on average or normal strings, it is virtually impossible to secure statistics exactly representative of field conditions, since it is inevitable that some rattles will be broken in the process of capturing the specimens, and, unless great care be taken, in their preservation as well. It is not satisfactory to utilize specimens that have been the subject of frequent examination in a museum, for rattles, softened by preservative, are particularly subject to breakage. Also, one must be careful not to utilize series of specimens in which there has been any conscious selection with respect to the length and character of the strings. For example, my own collection of preserved red diamond rattlers (*C. r. ruber*) would give an entirely erroneous idea of the proportion of unbroken rattle strings occurring in that species, since I have deliberately saved specimens with unbroken strings in order to accumulate certain dimensional data.

In tables 5:1 and 5:2, data are presented on two large series of rattlers often used for statistical data in my studies: the Platteville, Colorado, series of prairie rattlesnakes (*C. v. viridis*), and the Cape series of San Lucan diamondbacks (*C. r. lucasensis*). These were carefully handled during both capture and preservation, and are believed to be fairly representative of wild populations. Only adolescents and adults are included.

In statistics of this character it is necessary to take the season of capture into account, as well as the species of snake. The Platteville series were collected about their dens at the time of going into hibernation in autumn or emerging in the spring. At this season it will be observed that most of those with complete strings have 5 rattles. However, had the collection been made in the summer,

TABLE 5:1  
CONDITION OF RATTLE STRINGS IN THE PLATTEVILLE SERIES OF *C. v. viridis*  
(Adolescents and adults only)

Number of rattles	Complete strings			Broken strings			Total		
	M	F	T	M	F	T	M	F	T
0.....	...	...	...	2	3	5	2	3	5
1.....	...	...	...	1	6	7	1	6	7
2.....	...	...	...	6	9	15	6	9	15
3.....	1	1	2	15	17	32	16	18	34
4.....	10	21	31	53	33	86	63	54	117
5.....	69	69	138	53	42	95	122	111	233
6.....	8	20	28	46	37	83	54	57	111
7.....	9	12	21	43	12	55	52	24	76
8.....	4	2	6	8	5	13	12	7	19
9.....	...	...	...	2	1	3	2	1	3
10.....	...	...	...	1	...	1	1	...	1
Total.....	101	125	226	230	165	395	331	290	621

(M, male; F, female; T, sexes combined).

TABLE 5:2  
CONDITION OF RATTLE STRINGS IN THE CAPE SERIES OF *C. r. lucasensis*  
(Adolescents and adults only)

Number of rattles	Complete strings			Broken strings			Total		
	M	F	T	M	F	T	M	F	T
0.....	..	..	..	...	...	...	...	...	...
1.....	..	..	..	1	...	1	1	...	1
2.....	..	..	..	2	3	5	2	3	5
3.....	..	..	..	2	3	5	2	3	5
4.....	..	..	..	3	4	7	3	4	7
5.....	1	3	4	10	9	19	11	12	23
6.....	6	6	12	15	21	36	21	27	48
7.....	9	7	16	31	17	48	40	24	64
8.....	6	5	11	38	17	55	44	22	66
9.....	..	1	1	28	14	42	28	15	43
10.....	2	..	2	22	7	29	24	7	31
11.....	..	..	..	15	4	19	15	4	19
12.....	..	..	..	...	1	1	...	1	1
13.....	..	..	..	...	2	2	...	2	2
14.....	..	..	..	...	1	1	..	1	1
Total.....	24	22	46	167	103	270	191	125	316

(M, male; F, female; T, sexes combined).

6 or 7 rattles would have predominated. By the following hibernating date, were the strings complete, the same snakes would have had 7 to 9 rattles; but, as is seen, few retain such strings entire, for breakage is rapid after there are 8 in the string. Thus, in the table, these older snakes fall into the broken-string category.

Similarly, in the *lucasensis* statistics the table represents a spring series. Had the snakes been collected in the summer, strings of 8 and 9 rattles would have predominated among the complete strings. By the following spring these would become tens or elevens. But unbroken strings of this length are fragile and vulnerable, so that when next spring does arrive, few, if any, of the two-and-a-half-year-old snakes still have unbroken strings, and the 7 rattles of the one-and-a-half-year-old snakes of one year later would still set the mode at this figure.

Although the season of collection affects the mode of the complete strings, it is less likely to affect the broken-string category. For, if a rattler gets four new rattles per year, it is obvious that the modes in complete strings at any season will be four units apart. But breakage occurs irregularly, and once a string is broken the seasonal modes or peaks largely disappear.

That there is some sexual dimorphism in the retention of complete strings is evident from the tables. For example, 30.5 per cent of the male *viridis* had complete strings, while 43.1 per cent of the female strings were entire. In the *lucasensis* the corresponding percentages are 12.6 per cent for the males, and 17.6 per cent for the females. No doubt the higher breakage shown by the males results from their greater activity.

The lower percentages of unbroken strings in *lucasensis*, as compared with *viridis*, is a climatic effect. For *lucasensis* has a longer growing season and averages about 7 rattles (if the string is complete) in the spring, as compared to 5 in *viridis*. But a 7-segment string has a lower chance of survival without breakage than a 5-segment, other conditions being equal.

At this point, mention should be made of the fact that the button, being the thinnest and most fragile of the rattles, and having only one gripping edge, is the most easily lost. The subsequent rattles are successively strengthened, both by thicker and better reinforced walls, and, beginning with rattle No. 3 or No. 4, the second transverse groove is serviceable in gripping the succeeding rattle, so that the hold is doubled (fig. 5:14d). At about rattle No. 8 almost full adult strength and holding power are reached. This fragility of the early rattles, especially the button and Nos. 2 and 3, makes it clear why extra-long strings—say above 11 rattles—are so seldom unbroken. There seems no truth in Rivers' theory (1874, p. 507) that brittler rattles are produced as a snake ages; on the contrary, the later rattles are heavier and stronger than the earlier (see table 5:3, last column).

Although there is sexual dimorphism in the percentage of specimens having complete strings, there is no significant difference in the average length of the complete strings, the following being the figures:

Average Number of Rattles, Complete Strings			
	Males	Females	Both sexes
Platteville <i>viridis</i> . . . . .	5.25	5.22	5.24
Cape <i>lucasensis</i> . . . . .	7.16	6.78	6.98

Corresponding figures for the broken strings are as follows:

Average Number of Rattles, Broken Strings			
	Males	Females	Both sexes
Platteville <i>viridis</i> . . . . .	5.24	5.04	5.15
Cape <i>lucasensis</i> . . . . .	7.91	7.27	7.67

Hence, while more females retain complete strings, they do not average more rattles; this indicates slower female growth, or fewer skin changes at a given age.

It will be observed that there is little difference between broken and unbroken strings, as far as the average number of rattles is concerned. I should expect to find a somewhat higher average in the broken strings because of the greater strength in the terminal rattles. There is some indication of this in *lucasensis*. It must be recognized that the broken strings are penalized by having among their number several individuals with from 0 to 3 rattles; none with these low numbers is contained in the complete-string category, since they would be juveniles and therefore eliminated from the tabulation. If we begin with 4-rattle strings then, as expected, the broken strings have a higher average number of segments than the unbroken.

It must be remembered, with respect to statistics of this character, that string averages in the field are certain to be somewhat higher than those cited in these tables; however, in this case of these carefully handled series, the discrepancies are believed to be minor. But this cannot be said of the usual run of specimens in collections.

One point does stand out in the figures presented—namely, the definitely higher average of the *lucasensis* strings as compared with *viridis*. Differences such as this may be attributed to a variety of reasons: the comparative dispositions of the snakes; the prevalence of enemies causing the use of the rattle; the character of the country inhabited; and, finally, the relative strengths of the strings themselves.

An example of the first differential character may be observed in a comparison of the red diamond (*C. r. ruber*) and the southern Pacific rattlers (*C. v. helleri*) of San Diego County. In a given period, 21 of the former were secured with complete strings having in excess of 8 rattles; of *helleri* there were only 12. The total number of adults was about the same in the two species. *C. r. ruber* is probably the most placid of all rattlesnakes; *helleri*, on the other hand, is of a rather nervous temperament. As these two snakes live in the same surroundings, characterized by boulders and chaparral, it is to be presumed that disposition accounts, at least in part, for the differences in the lengths of the rattle strings.

As examples of the second effect—the lack of enemies—island species, such as the Tortuga Island diamond (*C. tortugensis*) and the Cedros Island diamond (*C. exsul*), may be cited. The former, especially, is characterized by long rattle strings. Out of 270 *lucasensis* with broken strings, only 4, or 1.5 per cent, had more than 11 rattles; out of 37 *tortugensis*, 7, or 18.9 per cent, had more than this number, including one with 15, one of the longest natural strings I have seen. Similarly, of the available specimens of *exsul*, 8.7 per cent had more than 11 rattles.

With respect to the character of the country, it has been noted, as might be expected, that snakes inhabiting sandy areas, such as the western diamond (*C. atrox*) in some parts of its range, and the sidewinder (*C. cerastes*), are often characterized by long strings. For they are less subject to wear and breakage than the rattles of the brush and rock dwellers; the latter not only suffer from abrasion, but are more likely to be caught in a forked branch or the cleft of a rock.

Finally, we have the matter of relative strength. I think it probable that the difference between the average length of *viridis* and *lucasensis* strings, to which attention has already been directed, largely results from this effect. It is true, of course, that the larger rattles are subject to greater amplitude of vibration and more friction, but they seem to be even more than compensated for these requirements by added thickness and strength. The smaller species, such as the pigmy rattler (*S. miliarius*), the central-plateau dusky rattler (*C. t. triseriatus*), and the Arizona twin-spotted rattler (*C. p. pricei*) rarely have strings, either complete or broken, exceeding 7 or 8 rattles. In general, where the other variables are equal, larger species of rattlers tend to have longer strings. Small rattlesnake species with proportionately large rattles, of which the tiger rattler (*C. tigris*) is the best example, often have long strings; for, in these, there is an abundance of structural strength, compared to the forces causing breakage.

It is of interest to note that in the Platteville series of prairie rattlesnakes (*C. v. viridis*), several of the effects which I have mentioned militate against long strings. In this series of 621 snakes (adolescents and adults) only a single snake reached 10 rattles; this was a broken string on a male snake; there were three snakes with 9. The longest complete string contained only 8 rattles; of these there were six, four males and two females. The correlation of body length with number of rattles indicates that many of these adults would have had strings far exceeding these in number, had they remained unbroken; in other words, it was not a size limitation that cut the long strings to such small numbers—rather, it was the natural wear and breakage.

Very short strings are also abnormal; thus out of 621 Platteville snakes (no juveniles included) five had no rattles, and seven only one, the attached rattle sheathing the matrix. These were noiseless and therefore useless strings. The five unfortunates had had their rattles (including the matrices) cut completely off; they showed by other scars that they had been “killed,” and their rattles removed as trophies, but had subsequently recovered.

It should be made clear that breakage in rattle strings is both normal and beneficial. Very long strings, say beyond 12 rings, cannot be particularly serviceable from the standpoint of a sound-producing apparatus, and might be a positive detriment, for the very length and weight would damp out the vibrations. Furthermore, they would tend to arch over and drag on the ground, notwithstanding the fact that the normal crawling posture of rattlers causes the rattles to tilt upward and avoid contact with the ground.<sup>11</sup> Probably a string of from 6 to 8 segments constitutes the most efficient vibrator. Thus it seems natural and advantageous that rattles should be lost; the long string is exceptional and actually detrimental.

Rattles are normally lost either through the wear incident to use—that is,

<sup>11</sup> Strings of the fantastic lengths already mentioned, such as those with 30 to 40 rattles, would certainly touch the ground as the snake crawled, and be quickly worn away.

by being rattled so much that they wear out—or by being scraped or torn by interfering objects. For example, if a rattle be caught in the fissure of a rock or the fork of a branch, the snake will give a violent twitch of its tail and the offending rattle will be snapped off. At the San Diego Zoo, captive rattlers with long strings have been observed to break rattles off by bending a string at a sharp angle when the snake's own body was resting on it, or by pulling the rattles out from under its own coils. Ortenburger (1930, p. 427) saw a northern black-tail (*C. m. molossus*) break a string in this manner.

The rapidity with which a loss of rattle segments can occur through excessive vibratory use has been observed in captive specimens. Those that are extremely nervous when brought in, and that fail to become inured to the presence of human beings, rattle for such long periods that the rattles quickly wear out, this being especially true of the terminal segments of long strings. But captivity does not invariably produce this effect; on the contrary, some strings longer than any carried by wild rattlers have been attained by captives, because those that lose their fear seldom rattle, and become so lethargic that they crawl about but little. As a result, the rattles are conserved, producing some phenomenally long strings not matched in nature, occasionally reaching 20 or even more before breaking. The record thus far at the San Diego Zoo was held by a timber rattlesnake (*C. h. horridus*) that had an incomplete string of 29 rattles at the time of its death. The records for complete strings are also likely to be made by captives, C. B. Perkins of the San Diego Zoo having reported the longest complete string (with the original button) of which we have knowledge. This was on a Tortuga Island diamond rattler (*C. tortugensis*) that was received in 1937 with a complete string of 5 rattles. By August, 1941, it had 18 rattles, with the button still intact. Shortly afterward the rattle broke, 11 segments coming off in one piece. Complete strings of 15 or 16 rattles are not exceptional among caged rattlers. Probably the best illustration of the string-prolonging effect of a quiet and well-adjusted captivity was noted in a brood of 9 western diamonds (*C. atrox*) born in captivity and raised by the late Grace Olive Wiley at the Brookfield Zoo. Four out of 9 of these snakes at the age of 27 months still retained complete strings, which numbered 14, 15, 15, and 15 segments. In addition, another with 15 rattles had lost only the button. Any one of these would have been virtually a record breaker in a wild rattler, yet here we find 5 in a single brood. Of course, it should be remembered that these rattlers, because of the lack of a winter hibernation and other conditions peculiar to captivity, grew these large numbers of rattles in much less time than would have been required under natural conditions in the wild. The longest unbroken strings that I have seen on live wild rattlers were on a San Lucan speckled rattlesnake (*C. m. mitchelli*), and on a red diamond (*C. r. ruber*) from Yaqui Pass, San Diego County. Each had 13 rattles, including the original button. It is probably no coincidence that *C. m. mitchelli* has unusually large (and therefore strong) rattles in proportion to the length and bulk of its body, and that *C. r. ruber* is exceptionally peaceable in disposition. Ross Allen sent me for examination the rattle of an eastern diamondback (*C. adamanteus*) comprising a complete string of 17 segments. This had been removed from a snake 1,362 mm. (53½ in.) long, captured in Marion County, Florida. The rattle was apparently authentic. As mentioned elsewhere, the longest in-

complete string I, myself, have seen on a wild rattler was 16 (this to be compared with the record, in my own experience, of a complete string of 13); and the longest apparently authentic, but incomplete, string I have examined, but not attached to the snake, was the western diamondback (*C. atrox*) string of 23 segments in the possession of Stanley Mulaik. This may be compared with Ross Allen's 17-segment complete string on an eastern diamondback. The corresponding record figures for captive rattlers were, as I have stated: incomplete string—29 in a timber rattlesnake (*C. h. horridus*); complete string—18 in a Tortuga Island diamondback (*C. tortugensis*).

#### CHEMICAL COMPOSITION

The rattle of the rattlesnake is composed of keratin, the albuminoid substance that is also the basis of such tough animal products, able to withstand wear without further nourishment, as horn, hair, nails, and feathers. A chemical analysis of the rattle material, together with comparative analyses of rattlesnake skin and other substances, will be found on p. 321.

It is of interest to note that as early as 1709, Lawson (p. 128) had stated that the rattle material resembled that of horns or human nails. This was repeated by Brickell (1737, p. 142). Lacépède (1788–89, vol. 2, p. 396; Kerr's translation, 1802, vol. 4, p. 252) thought the composition the same as that of the rattlesnake's scales and plates. Hopley (1882, p. 297) likened it to hair, nails, quills, or hardened skin; and Mole (1895, p. 191) to the material of human nails.

#### STRUCTURE OF THE RATTLE

The knowledge of the structure of the rattle, as divorced from the histology of its formation and the chronology of its growth, has been a gradual development. Some of the early landmarks in this research were the descriptions and sketches of Grew (1681, p. 50), Tyson (1683, figs. 10–12), Catesby (1743, vol. 2, plate 41), Lacépède (1788–89, vol. 2, p. 396; Kerr, vol. 4, p. 252), and Bosc (1803, p. 551). These revealed how the successive lobes or elements fitted into each other. I shall make no further attempt to outline the history of the accumulation of the knowledge of the rattle structure, but shall repeat, with appropriate modifications, my own description from a prior publication (1940b, p. 35).

The rattle is too irregular an object to permit a universally satisfactory description; however, certain generalizations may be made. It is known, of course, that, as the rattle is carried by the snake, the greater dimension of each ring is vertical and the lesser transverse; that is, the rattle is carried with the broader, flatter sides as lateral faces. In addition to the deep transverse grooves, or constrictions, that separate the lobes of each rattle, there is a secondary longitudinal furrow, sometimes narrow and sharply indented, more often broad and shallow, along the lateral faces of the exterior lobes. The longitudinal groove of each superior lobe loosely engages the groove in the inferior lobe beneath; thus it affords a certain stability by guiding movement, and, by its corrugation, increases strength. In the hidden lobes, the longitudinal grooves are deep and sharply angular, so that the engagement of the groove of the second lobe with that of the third is quite restrictive. Often these internal furrows are so deep and compressed as to produce internal reinforcing fins.

The configuration that permits the snake to keep its rattles clear of the ground as it crawls, is the result of an asymmetrical development above and below the longitudinal furrow (figs. 5:6 to 5:8).<sup>12</sup> Necessarily there is a looseness of fit in the coupling of the successive segments to allow for the movement whereby the successive elements may strike each other and produce the sound. Were the rattle constructed symmetrically about the longitudinal center line, this looseness would

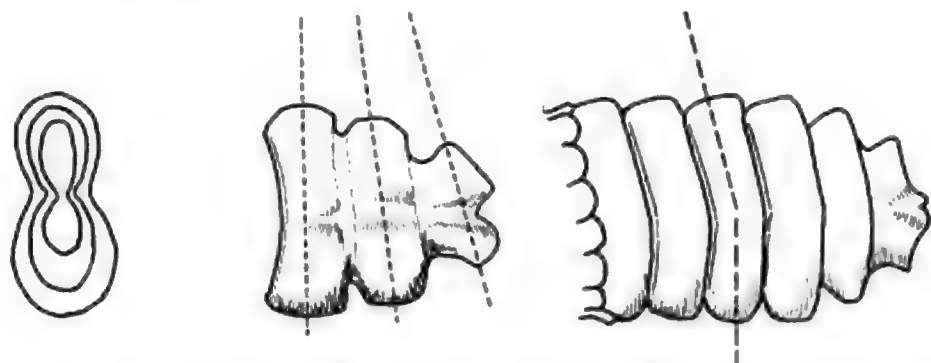


Fig. 5:6 (left). Vertical section showing the asymmetry of the internal fit of three interlocking segments of a rattle.

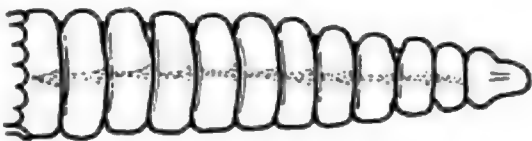
Fig. 5:7 (center). Lateral asymmetry of a rattle segment.

Fig. 5:8 (right). Forward slope of the upper lobe of a rattle segment.

Fig. 5:9. Rattle-string with the outer end raised to its highest position, to show the effect of the asymmetry on the possible travel.



Fig. 5:10. The same rattle-string as in figure 5:9, with the outer end in its lowest position.



result in a downward curve, which would allow the posterior rattles to drag. But the rattles are not symmetrical; on the contrary, each ring is so distorted that, when the rattle string is in a position permitting equal degrees of freedom both upward and downward, the center line is a curve upbending posteriorly (fig. 5:9). When the limit of travel downward, as permitted by the successive interlocks, is imposed by the weight of the rattle, the center line is virtually straight (fig. 5:10). By this means a slight upward tilt of the tail end suffices to keep the rattle clear of the ground, and this is the snake's normal crawling posture (fig. 6:5).

The configuration whereby the asymmetry is produced is complicated and ingenious. Each flat side of a rattle is grooved by the central longitudinal furrow.

<sup>12</sup> The asymmetry was mentioned by Hopley (1882, p. 306); she failed to understand how it was made effective. Of this, Quelch (1891, p. 6) has given a brief and correct explanation.

This is rounded, and may be wide or narrow in the anterior surface lobe, but in the concealed lobes it is deep and with sharp angles. This furrow serves both as a reinforcement of what would otherwise be a weak, flat surface, and as an interlocking guide between the meshing lobes. Thus each lobe is virtually divided into two halves; looked at endwise the halves appear like intersecting cylinders. So deeply cut by the side grooves is the innermost lobe, that, from the end, the two cylinders seem connected only by a thin, vertical web. The important point with reference to the asymmetry is that the upper half of each exterior lobe is smaller than the lower half, while the upper halves of the interior lobes are larger than their lower counterparts. Thus the fit in the upper half between the exterior and interior lobes is closer than in the lower halves, and the limit of travel in any direction is first reached in the upper half (fig. 5:6). This is further accentuated by a longitudinal compression of the transverse grooves and lobes in the upper half as compared with the lower; each separate rattle is therefore curved slightly upward as if it were a segment of a circle of large diameter (fig. 5:7). In large specimens, a third, but related, type of asymmetry is clearly evident; this is a forward slope of the upper lobe, which is at an angle with the lower (fig. 5:8).

The effect of the asymmetry can best be visualized by the following simple experiment: First, hold a long rattle string in the position as it is carried by the snake and it will be observed that it remains straight (fig. 5:10). Now turn it upside down and the whole structure sags; if the string be long enough, the last links will hang vertically downward (as in fig. 5:9, were it upside down). Another method of showing that the mid-position of a rattle string is a curve, is to press the two ends of a long string toward each other so as to reduce the longitudinal lost motion to a minimum. It will be found that the string assumes a curve, with the end tilted upward.

Not only is this asymmetry important in procuring a safe carrying position, but, also, it has a beneficial effect in sounding the rattle. When the rattle is to be vibrated, the maximum effect will be produced, with the least wear and consumption of energy, if the several clashing elements are balanced on their center lines. Were the rattle symmetrical, the tail would have to be vertical to secure this balance, and the rattles would tend to fall in a curve either forward or back. But, owing to the asymmetry, an angle of some  $80^{\circ}$  from the horizontal will suffice to hold the rattles in a straight line, and this is the angle at which the rattler in the striking coil usually sounds its rattle (fig. 7:2). Occasionally, however, it will be held farther from the vertical, but still the asymmetry keeps the string straight instead of drooping.

The articulation of the rattle is necessarily loose, yet it is surprising how difficult it is to remove successive rings, particularly adult segments with a full complement of transverse grooves, so effective is the clinch or interlock (figs. 5:11 and 5:12). The fracture and complete removal of an exterior lobe at the center of a string will not cause the loss of the rattles posterior thereto, as they are still coupled by the smaller and stronger lobes within. So rattles, unless cut or broken clear through, must be worn off and lost in succession from the posterior end forward, and each lobe of a segment must be completely fractured before detachment finally occurs. Hence we see how these relatively fragile members are so tenaciously retained.

As an indication of the looseness of the articulation, it may be noted that a string of rattles from an adult southern Pacific rattler (*C. v. helleri*), the rattles being 12 mm. in width and 42 mm. in length when adpressed, measured 48 mm. when fully extended, thus showing a longitudinal lost motion of 6 mm., or 13.3 per cent of the normal string length of 45 mm. A string of 12 eastern diamond-back (*C. adamanteus*) rattles 78 mm. long had a lost motion of 12.8 per cent; and a set of 15 Tortuga Island diamond (*C. tortugensis*) rattles 86 mm. long, 8.3 per cent. All of these strings were fully adult, that is, the posterior rattles were of substantially the same size as those next the body.

In all rattles, the interior lobes are more sharply angular than the larger, outer lobe. There is a bead, or narrow outward curl, along the lateral anterior edge of

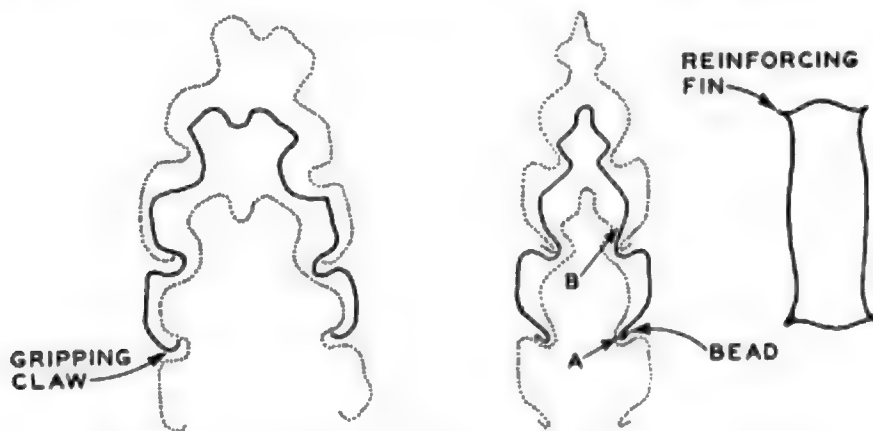


Fig. 5:11 (left). Vertical cross section of interlocking rattles (two-dotted to facilitate identification).

Fig. 5:12 (center). Horizontal cross section of interlocking rattles, through the center of the lower halves of the lobes.

Fig. 5:13 (right). Vertical cross section of a lobe at the bottom of the anterior groove, showing the reinforcing fins.

each rattle. Usually this bead is doubled back and flattened against the rattle to form a sort of hem or selvage, a device beautifully fashioned to prevent the start of a tear (fig. 5:12). Also, as this folded edge strikes against the shoulder of the next anterior rattle, it comprises one of the contacts producing the noise; thus the bead becomes a reinforced wearing surface (point A, fig. 5:12). The other principal point of contact is between the heavily stiffened posterior lobe and the transverse groove of the outer rattle (point B). These contact points produce the maximum noise with the least friction and wear.

Another ingenious development is the reinforcement of the transverse grooves between lobes by tiny ribs at the four corners, for these grooves, as viewed in section, approach a rectangular, rather than an elliptical, shape (fig. 5:13). Between these ribs, at top and bottom, the interlocking clasp of the first lobe is particularly effective, the grip being almost clawlike (fig. 5:11); at the same time it acts as a hinge, permitting unimpeded side movement in the direction taken by the vibrating rattle.

An outline of the changes in size and shape, in the successive segments of a string, can best be exemplified by a description of the elements of a typical unbroken string. A 10-rattle western diamond (*C. atrox*) string was selected for this study.

*Unit A* (prebutton, fig. 5:14a). (This is a hypothetical description of this unit, since it disappeared with the first shedding after birth. It is described from specimens of recently born young.) This is flat and single-lobed. The vertical cross section is elliptical. The central longitudinal furrow is evident but not deeply indented. The material is thin, flexible, and transparent, and the entire rattle is rather easily removable because it is only slightly constricted at the clinching end. It does not tear easily. From a side view, the posterior end is semicircular in outline. The thickness of material is about 0.015 mm.

*No. 1* (button, fig. 5:14b). There are two lobes only, and these not sharply differentiated; both are smooth and rounded in outline. The anterior constriction

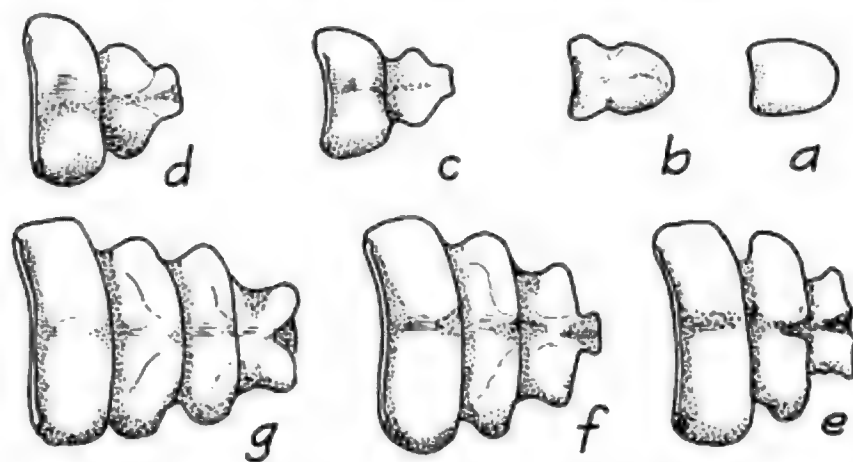


Fig. 5:14. Example rattle segments from an unbroken rattle-string of a western diamond rattler (*C. atrox*.)

- a. Prebutton (hypothetical, because it is lost with first shedding of the skin)
- b. Button
- c. No. 2 rattle
- d. No. 3 rattle
- e. No. 6 rattle
- f. No. 10 rattle
- g. A four-lobe segment (hypothetical, because rattles do not invariably attain four lobes)

is adequate for holding and a slight bead is evident on the edge. The groove between lobes, while distinct, is shallow, particularly on the sides, and not clearly defined. The longitudinal furrow is continuous from end to end and is deeper posteriorly, thus pinching the end into upper and lower sections. A vertical asymmetry is already in evidence, the transverse groove being deepest above.

*No. 2* (fig. 5:14c). Of this rattle, the second (or posterior) lobe is completely developed and the first transverse groove sharply cut. The third lobe is in evidence, but has no holding power. The bead on the first, or anterior, lobe has become folded into a hem.

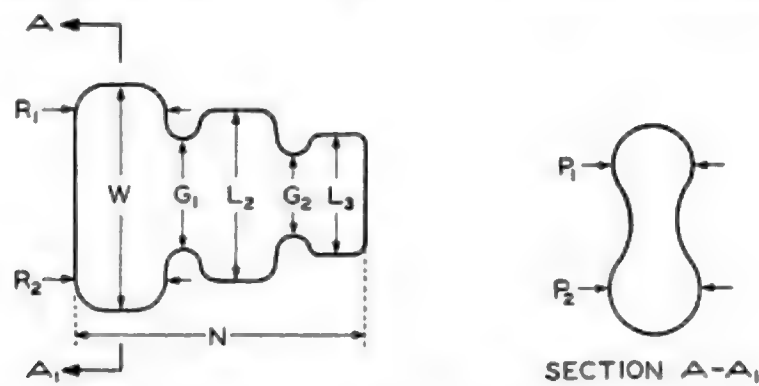
*No. 3* (fig. 5:14d). There is little change from the previous rattle except that the third lobe is better developed; it takes the form of two parallel horizontal cylinders connected by a web. The vertical asymmetry is more in evidence.

*No. 4*. Of this rattle, the posterior (or third) lobe is considerably enlarged by the outward divergence of the two cylinders; it now has considerable holding power, which is of importance in retaining rattle No. 3. The reinforcing ribs at the corners of the transverse grooves are clearly in evidence, but more so in the anterior groove between the first and second lobes. Viewed from the interior,

these ribs are seen to be of importance in strengthening the structure. The clinch of the first lobe is particularly effective at the vertical claw, which grips the groove between the corner reinforcements of the second lobe of the No. 5 rattle.

No. 5. The third lobe is now structurally of considerable importance. Viewed from the posterior, so that each lobe appears as a small circle, concentric with its larger anterior fellow, it can be seen that the anterior or outer lobe has a larger lower than upper segment, while the contrary is true in lobes two and three.

TABLE 5:3  
DIMENSIONS OF A RATTLE-STRING OF A WESTERN DIAMOND RATTLESNAKE (*C. alrox*)



Rattle number	W	L <sub>2</sub>	L <sub>3</sub>	G <sub>1</sub>	G <sub>2</sub>	N	R <sub>1</sub>	R <sub>2</sub>	P <sub>1</sub>	P <sub>2</sub>	Wall Thickness
1	64	51	..	47	..	82	29	31	40	45	0.23
2	75	50	29	39	27	87	38	34	46	53	0.25
3	88	63	31	44	25	97	43	40	56	60	0.28
4	103	75	39	55	31	113	45	44	60	68	0.31
5	117	90	54	66	41	117	48	43	69	75	0.36
6	127	100	63	73	49	123	50	46	73	81	0.43
7	133	106	73	77	56	122	48	43	76	84	0.36
8	139	116	78	85	60	120	49	44	75	83	0.43
9	144	123	88	88	69	133	50	46	78	85	0.46
10	156	126	93	94	71	146	55	50	82	92	0.51

Note: All dimensions in tenths of a millimeter.

No. 6 (fig. 5:14c). The third lobe is still further enlarged. The posterior surface of the middle lobe is deeply indented.

No. 7. The transverse grooves are still deeper and more sharply indented.

No. 8. There is little change beyond an enlargement of the parts.

No. 9. Now, for the first time, the divergent cylinders that constitute the posterior lobe are extended into little cones as if a fourth lobe were in contemplation. The transverse grooves are deep-set and angular, and the symmetry more than ever evident.

No. 10 (fig. 5:14f). This rattle, the proximal or attached rattle of the present string, surrounds the matrix from which it has only partly sprung away. The tentative conical extensions from the rear of the posterior lobe have become more prominent.

Dimensional data on this typical string are set forth in table 5:3. It is of interest

to note the gradual increase in the wall thickness, which was measured at the flat face of the outer lobe of each segment.

Whether, had this string grown further, a complete fourth lobe would have been developed, is not known. Four full lobes are occasionally found (fig. 5:14g), particularly in the larger species, and sometimes the beginning of a fifth has been observed. I have been unable to determine whether the development of a fourth lobe is characteristic of a particular age, sex, or species—the indications are rather against consistency on this point. I have seen some long strings of 12 or more rattles in which the oldest showed by its form that it was an adult ring, thus indicating that the youngest was at least rattle No. 20, yet no fourth lobe had begun to form. So it appears that 3-lobe segments are typical of most adult rattles. The second lobe is evident, but not serviceable, in the button; it becomes effective in rattle No. 2. The third lobe normally is evident in rattle No. 2, and first becomes truly effective in rattle No. 4. By the time rattle No. 7 is attained, the adult shape is reached. Thereafter the increase in the size of successive segments is much slower; this increase continues at least until the twelfth or fourteenth rattle, and possibly beyond; however, after the twelfth the increment is so small as to be masked by seasonal fluctuations.

At the beginning of this discussion of rattle structure, I mentioned the fact that the rattles on the snake are always attached and carried by the snake with the broad or major face vertical. Tyson, as early as 1683 (p. 54), pointed this out, but it is surprising how frequently this easily verified feature still constitutes a source of argument in the question-and-answers columns of the sporting press—an argument that will never end. A theory frequently advanced is that mountain rattlers wear their rattles with the broad face vertical, while in plains or prairie snakes the broad side is horizontal (Anon., 1872b, p. 642; Bailey, 1876, p. 404). A variation expressed by a magazine editor was to the effect that eastern snakes carry their rattles flat side down and western, flat side vertical (Moran, 1878, p. 341). Still another view credits the females with vertical and the males with horizontal rattles (*Outdoor Life*, vol. 50, no. 3, p. 233, September, 1922). This myth is sometimes reversed, the female having the horizontal rattle. Other discussions of this feature are those of Moody (1907, p. 533), McCandless (1907, p. 1012), and Jaques (1908, p. 91).

It is probable that this uncertainty arises from an examination of dead snakes, in which the tail has become so limp or damaged that it is not clear how the rattle was carried. Anyone making a careful examination of the rattles of any live rattlesnake of either sex, and of any known species, will be quickly convinced that the flat side is always perpendicular to the ground. Even in dead specimens, this can be verified if one notes the relationship of the rattle to the scales (the subcaudals) on the underside of the tail, which are much larger than the scales on the top or sides of the tail.

#### THE SHIFTING PROCESS

The mechanism whereby each rattle segment is, in the course of its formation, displaced one lobe forward—or, what amounts to the same thing, the next older rattle is transferred one lobe back—is a complicated one. The fact of displacement has long been understood, for this is basic to the loose fit yet mechanically

tenacious interlocking of the successive segments, upon which the efficient operation of the rattle as a sound producer depends. Early explanations merely stressed the interlock; later ones attempted to explain the shift, none with great success, for it is further required that the interlock be never relinquished during the shifting process or all the rattles would be lost. Such explanations have been made by Lacépède (1788–89, vol. 2, p. 403; Kerr's translation, 1802, vol. 4, p. 255), Czermak (1857, p. 294), Wyman (1862, p. 121), Garman (1887, p. 2), Quelch (1891, p. 2), and Klauber (1940b, p. 31). More recently Zimmermann and Pope

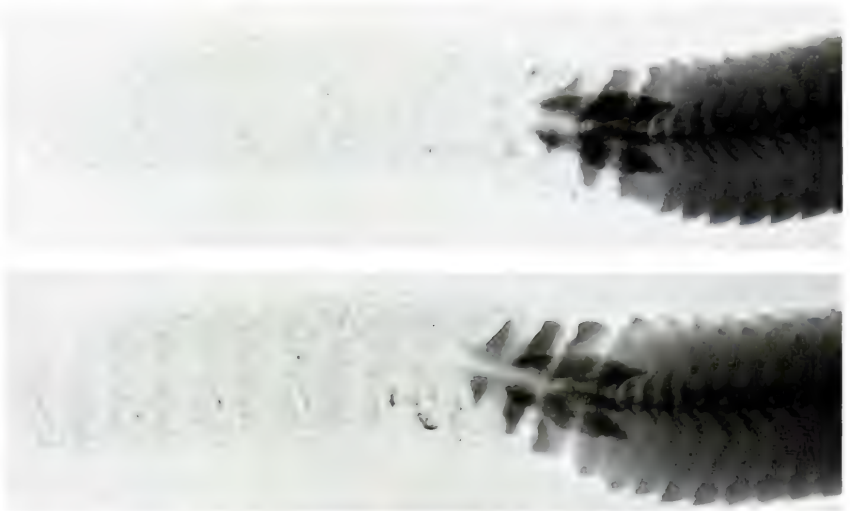


Fig. 5:15. Mojave Desert sidewinder (*C. c. cerastes*), showing lack of a rattle, probably a congenital defect. (Specimen collected by Charles E. Shaw and the author at Shoshone, Inyo County, California, on the night of June 4, 1949. Photograph by G. E. Kirkpatrick.)

(1948), by the use of X rays, clearing and staining, and advanced histological techniques, have done much to explain the mechanism of the shift, as well as the histological processes upon which it is dependent.

They divide the cycle of the formation of one complete segment into two periods, an active and a latent period. During the latent period, as implied by the term, no progress in rattle formation is evident; this is a period of normality or rest. In one cycle of 77 days cited by the authors, the latent period entailed about 60 days, or 78 per cent of the cycle. This was followed by an active period involving the formation of a new rattle, a period which the authors have further subdivided into an accretion interval of about 14 days, and, finally, a resorption period of 3 days. It may be assumed, although not so stated by the authors, that the great differences in the observed time-lengths of the shedding cycles of rattlesnakes—50 days to a year or more—are absorbed in variations in the latent, rather than in the two sections of the active period. This is indicated by the fact that the extent of the active period of shedding, as measured from the initial "blue-eyed" stage to final exuviation, is apparently not lengthened when the entire shedding cycle is lengthened, although this may not be entirely true of frequently shedding young snakes.

The growths and movements that take place during the active period have been excellently illustrated by Zimmermann and Pope (pp. 370-72) in series of X-ray pictures of the tail, matrix, and rattle of an adult western diamond rattler (*C. atrox*). Two of these figures are reproduced here as figures 5:16 and 5:17, through the courtesy of the authors. During the latent period, the proximal or attached segment closely hugs the matrix on which it was formed, and the two posterior prongs of the bony shaker extend almost to the posterior tips of the distal lobe of the matrix (fig. 5:16). With the onset of the initial stage of the active



Figs. 5:16 and 5:17. X rays of the rattle matrix and shaker of a western diamond rattlesnake (*C. atrox*), showing the change in the position of the bony shaker in relation to the tissue of the matrix. Fig. 5:16 (above) represents the beginning of the latent period; fig. 5:17 (below), near the middle of the accretion period. (Figures through the courtesy of Dr. Arnold A. Zimmermann and Mr. Clifford H. Pope.)

period, a new lobe of the matrix begins to form at the forward edge of the existing rattle, where there is a crease (called the *sulcus* by the authors) between the edge of this rattle and the tissue of the tail (fig. 5:17). This new lobe swells during the entire period of accretion; externally its presence gradually becomes apparent by the stretching of the old skin that covers it, the folds between the scales of this skin being flattened out to permit stretching. Zimmermann and Pope (p. 368) emphasize the fact that the growth of the new lobe never encroaches on the tail itself; on the contrary, it leads to the only other possible result—a shift tailward of the soft tissues along the shaker. (The old skin does not pull away from the previous rattle, since its end is caught and held by a fold or selvage in the proximal edge of the rattle; if it did pull away it would uncover the newly forming lobe beneath, to the detriment of the latter.) With the growth of the new lobe, the matrix becomes temporarily 4-lobed, and is extended backward until the shaker is seen to form the core of the anterior 3 lobes, instead of the posterior 3 (there was no fourth then) as it did at the beginning of the process. Thus, if we use the position of the shaker as a guide point or bench mark, it will be seen that the posterior 3 lobes of the matrix, carrying with them the old cornified

rattle segment that surrounds them, have been pushed back one lobe. At the climax of the period of accretion, the two anterior lobes of the temporarily 4-lobed matrix do not differ greatly in size.

Then follows the period that the authors designate as resorption, during which the 3 posterior lobes shrink by having their tissues reabsorbed into the body. The former distal lobe disappears entirely; what was formerly the middle lobe takes on the size and shape of the distal lobe that has disappeared; and the former third lobe shrinks into a new second. Once more there is a 3-lobed matrix, almost exactly the same in size and shape as the one that existed before the period of accretion began. There follows the keratinizing process on the surface of the matrix, thus producing a new rattle segment, after which the snake sheds and, for the first time, the proximal lobe of the new rattle is disclosed. Unfortunately, the X-ray pictures do not show the progress of keratinization, since X rays fail to differentiate between a keratinized surface and the connective tissue beneath.

This description covers the formation of a new rattle on an adult snake, in which successive segments are alike in size and shape. In the case of adolescent snakes, the resorption is not complete, so that after each resorption the matrix does not return to its original form, but, with each cycle, becomes longer and larger, likewise changing from an original single lobe, through a 2-lobe, to its eventual 3-lobe form. Permanent 4-lobe matrices in some snakes are not unknown; these must be 5-lobed during the accretion period.

In my own former description of the shifting process (p. 32) I attributed the decrease in size of the posterior lobes, following the shift, in part to desiccation, basing this opinion on the presence of a jelly-like material found between the shrinking lobes of the matrix and the rattle surrounding them. Zimmermann and Pope (p. 392) consider this material to be the disintegration products of the disappearing *stratum intermedium*. Also, they find (p. 372) no evidence (as I had suggested) of a flow or longitudinal displacement of soft tissues within the epidermal covering and the newly forming horny segment. Instead, there is a withdrawal shrinkage, after the soft tissues of the end body have moved caudad. It seems to me that such a distinction is hardly justified by the terms used, for what is a withdrawal (resorption) if not a longitudinal displacement of soft tissues?

There is one other important feature of the shift mechanism that Zimmermann and Pope have failed to clarify, namely, the reappearance of any defect—such as a deep crease or a splinter—at exactly the same point on each succeeding lobe of a rattle string. It was in an endeavor to explain this frequently observed condition that I evolved a wave theory of the skin of the matrix to which they object. They state (p. 370) that “the epithelial covering remains intact as the living *stratum profundum* on the rapidly shrinking lobe. In contrast, the *stratum corneum* becomes detached and remains behind to constitute the new horny segment of the rattle.” It is the *stratum profundum* that carries any defect repeated in each corresponding lobe of successive rattles; and the question seems to me still unanswered as to how a defective point on, let us say the *stratum profundum* of the middle lobe of a segment, can get to the same point under the middle lobe of the following segment without at some brief period occupying the transverse furrow between lobes 2 and 3 of the transitional 4-lobe matrix. This movement I described as a wave action. This requirement needs further experiment and clarification.

Functionally, the close adherence of the attached rattle—the recently keratinized *stratum corneum*—to the matrix during the latent period is important, since it forms a protective sheath for the matrix and the skin that covers it. Were the fit loose, there would be wear on the matrix whenever the snake rattled.

#### HISTOLOGY OF RATTLE FORMATION

Zimmermann and Pope (1948, p. 386) have made important advances in the understanding of the cytology and histology of rattle formation; however, it is regrettable that their researches of these phases of rattle development were in large part made on the rattles of young snakes, and that a discussion of the homology of rattle formation, correlated with the formation and character of the skin elsewhere on the body of the snake during a shedding cycle, was not presented. That there is such a homology, therefore proving—were any further proof deemed necessary—that rattle formation is in synchronism with exuviation, is their conclusion. Their failure to recognize the prebutton somewhat reduces the value of their discussion of the early development of the matrix in the button state (p. 376).

As is the case with ordinary reptilian skin formation, the lower layer of the epidermis, known as the *stratum granulosum*, differentiates into two primary layers, the *stratum profundum* and *stratum corneum*. (The *stratum profundum* in turn comprises two sublayers, the *stratum basale*—or *stratum germinativum*—and the *stratum spinosum*.) The *stratum corneum*, as it differentiates from the *stratum profundum*, keratinizes and is ready to become the exterior wearing surface, after which the old skin is shed, and the *stratum intermedium*, which separates the new *stratum corneum* from the old, disappears through degenerative processes. This degeneration of an intermediate layer between the new and old corneous strata facilitates shedding. Zimmermann and Pope show that, at least in the case of the rattles of young snakes, the keratinizing of the *stratum corneum* does not occur simultaneously throughout a new rattle but begins at the distal end and progresses forward, the process being closely related to the rattle shift occurring during the final phase of the resorption process.

Zimmermann and Pope find no evidence of a change in the size of a rattle during keratinization, by reason of drying or any other external effect; the size and shape of the rattle are determined entirely by the shape of the matrix upon which it is molded (p. 367). To future histological workers, it may be suggested that parallel studies be made of the progressive changes in the *stratum granulosum* of the tail and of the matrix to determine the reason for the great difference between the two corneous layers, one of which is thin and flexible (the snake's skin), the other thick and stiff (the rattle).

As a matter of fact, the proximal or attached rattle, even after the process of kernatinization is complete, is not exactly the same as the older rattles, for it is quite colorless and transparent, whereas the others are only translucent, and vary in color from straw to dark brown, depending on the species of rattlesnake. Whether this change results from oxidation or abrasion remains to be determined. The change takes place gradually during the normal or latent period, and darkens the anterior lobe especially, for this is more exposed than the others.

## THE SHAKER OR STYLE

The shaker or style, the specialized terminus of the vertebral column comprising coalesced vertebrae, is a characteristic and important element of the rattle structure. It was first studied by Czermak (1857, p. 295), and later by Garman (1889, p. 173), who concluded that the terminal vertebrae were distinct in embryonic rattlers, coalesced at the button stage, but were subject to further co-ossification and modification in shape during the subsequent growth of the snake.

By far the most important studies of the shaker thus far made, were those of Zimmermann and Pope (1948, p. 374). Equipped with the modern techniques of X rays, and clearing and staining, they were able to extend greatly the knowledge of the development of the shaker. Having adequate material, they could follow this development from the embryonic stage to that of young adults, noting the gradual change by the consolidation of the bony elements, including both the fusion of the previously separate terminal vertebrae and the accretion of extravertebral bony elements.

They found that in the massasauga (*S. catenatus*) the vertebral coalescence takes place postnatally, while in the two species of *Crotalus* that they studied, the eastern and western diamondbacks (*C. adamanteus* and *C. atrox*), the fusion was more advanced in late embryos than in postnatal *catenatus*, a considerable coalescence of 8 to 10 vertebrae having taken place within the matrix. These differences suggest the desirability of carrying the research into other forms in the hope of solving various phylogenetic problems. *S. miliarius*, *C. durissus*, *C. triseriatus*, *C. pusillus*, *C. pricei*, *C. lepidus*, and *C. stejnegeri* should prove especially worthwhile.

In the adult snakes the co-ossification is so complete that the style is relatively homogeneous. It is shaped somewhat like an arrowhead, with the proximal end notched where it engages the last unmodified vertebra; however, the distal point is branched or doubled vertically, one branch entering into each half (upper and lower) of the terminal lobe of the matrix (figs. 5:16 and 5:17). By reason of the extravertebral bony additions, the shaker is much wider (vertically) than the vertebrae it has replaced, thus occupying much of the central space of the matrix, and forming a heavy and rigid central core, which is further stiffened by a thickening of the upper and lower edges. There is usually a slight depression in these edges corresponding to the groove between the anterior and middle lobes of the matrix. The rigidity of the matrix is a feature of importance, not only as a transmitter of the tail vibrations via the connective tissue to the rattle, but also as a firm foundation for the periodic changes in the matrix required by the rattle-shifting process. Flexibility in the shaker, and therefore in the matrix, would lead to poor articulation between successive rattle segments. According to Zimmermann and Pope, the vibratory muscles are inserted in the base of the shaker; and its point of contact with the last normal vertebra is the pivot of vibration. Six bundles of muscles comprise the vibratory mechanism, three on either side.

## DIMENSIONAL RELATIONSHIPS

## RATTLE DIMENSIONAL VARIABILITY AND SEGMENT CONTINUITY

Up to this point I have dealt mainly with the function and structure of the rattle, but have supplied few data on the dimensional relations between successive segments, or the correlation between rattle and body growth. The rattles of the various species of rattlesnakes differ in these relationships, but before discussing these species differences, which are of decided taxonomic and phylogenetic interest, it is necessary, first, to determine the general principles involved in the size relationships of the successive segments of a string, and the variability in the dimensions of the rattles of a homogeneous rattlesnake population.

We have, in the rattle, a mechanism—possibly unique among the vertebrates—which, by the entire separation of successive elements from the body, renders such elements independent of succeeding bodily growth, or other changes except loss or destruction. Thus we have a series of chronological bench marks, and if we can determine the chronology of this separation, we may be able to learn something of the rate of bodily growth.

When we consider the statistics of the rattle, there are an embarrassing number of variables to untangle. Not only are there the differences of species and geographical races, but those of sex, rattle dimensions, and rattle-number, that is, its serial number in the order of acquisition or position in the string of rattles. The rattle dimensions may involve length, width, breadth, and thickness of material, and these may be correlated with snake length. The rattle-numbers may be expressed in terms of complete or broken strings.

In the selection of a representative dimension of each segment, with which other variables might be correlated, it was found that the dorsoventral width—that is, the maximum dimension across the visible, or anterior lobe—constituted the measurement most easily and accurately determined, and, when comparisons were to be made, this has been taken as the basic measurement representing each segment. As a rattle segment is asymmetrical, the axis across which the width is measured is not exactly perpendicular to the longitudinal axis of the string, but tilts slightly forward above (fig. 5:2).

The rattle-number is taken as the position of each segment in the sequence, the first permanent rattle (the button) being considered as No. 1, the next anterior rattle as No. 2, etc. At once we are confronted with the problem of whether it is possible to determine the position of a segment in the sequence, and therefore its rattle-number, if the button—with or without one or more of the succeeding terminal rattles—is missing. It has been found that one cannot place with certainty the position of a broken string by measuring the width of the several rattles, and comparing these measurements with those of known complete strings, since there is some overlap in dimensions. To be specific, even in a single species from a limited territory, there will be found, on some specimens, No. 5 rattles that are larger than the No. 6 rattles on others; and other No. 5's smaller than the largest No. 4 rattles of some other snakes. However, in the case of almost-complete strings, wherein only the button or, at most, 2 or 3 rattles are missing,

one can judge with considerable accuracy the position of the remaining rings in the original complete sequence, both by reason of the configuration of the incomplete terminus, and because the rapidly increasing sizes of the earlier rattles produce less overlap in the dispersion of dimensions.<sup>13</sup> But even in this case accuracy cannot be always assured, for occasionally a string is found that seems to contain an extra segment; that is, a segment involving no growth, yet inserted at a point in the string where a decided increment would be expected. When this occurs, the dimensional positions of all the succeeding segments deviate from the normal.

When the string begins to approach parallelism, or uniformity in the sizes of successive segments, which occurs when the adult stage is reached, the determination of the sequence is quite impossible, since the dimensional differences of successive rings are small, and there are random fluctuations in size, rather than orderly growth. For these reasons, in the observations that follow, where the rattle-number is used as indicating the position of a segment in the sequence, it is to be understood that an unbroken string was available, except for a few specimens wherein only the button was missing. The latter condition can usually be diagnosed with certainty by the shape of the string and the configuration of the exposed end of the No. 2 rattle. In the case of one subspecies, the San Lucan diamond (*C. r. lucasensis*), with unusually favorable material available, broken strings were diagnosed so as to carry the growth-trend statistics to longer strings than is possible solely by the use of unbroken strings.

To simplify the discussions that follow, I shall use the letter *W* to designate the dorsoventral width of any segment (fig. 5:2), *N* the rattle-number (known only in a complete string), and *L* the length over-all (snout to proximal edge of the basal rattle segment) of the snake.

Before attempting to interpret the statistics of rattle differences, we must first be assured that the results are not affected by certain conditions inherent in the method of making the measurements. Since most of the measurements were made on alcohol-preserved specimens, it is necessary to determine whether the dimensions are affected by this method of preservation. Specimens totaling 74 strings were calipered before and after preservation and a minor expansion resulting from the preservation process was noted, the average change being an increase of 0.78 per cent. This error is below those to be expected from other sources, in the measurement of so irregular and flexible an object, and it is therefore disregarded.

Next we must determine whether there is a conspicuous difference in size between attached and cast rattles of the same sequence number. In other words, is the fifth rattle larger or smaller when it has been cast free, than it was when still surrounding the matrix? Such a difference between proximal and cast rings of the same rattle-number might be the result of any of three causes: (1) Growth in the rattle between the time it is first bared and the time it is cast loose; (2) an internal pressure of the matrix upon which the attached rattle rests, causing it to be stretched beyond its final dimensions, or an internal adherence producing a contrary effect; (3) a shrinkage (or expansion) resulting from the preservative's having affected the attached rattles to a more important degree than those already cast off.

<sup>13</sup> This assumes the availability, for comparative purposes, of adequate numbers of complete strings from the same subspecies and from the same area.

These possible effects of casting a rattle free can be investigated only in a large and homogeneous group. For this, the Platteville series of prairie rattlers (*C. v. viridis*) was particularly suitable, as it contains no less than 452 specimens with complete strings, and in these the dimensions and rattle-number of 1,438 rings could be determined. In order to eliminate any possible effects of sexual dimorphism, the sexes were segregated. Comparisons were made, for each rattle-number, of the average dimensions of the attached and cast rattles. Out of 14 groups (rattle-numbers 1 to 7 for each sex), it was found that in 8 groups the attached rattles averaged larger than the cast, while in 6 the contrary was true. The differences were small and followed no particular order. It was therefore concluded that the attached rattle has the same dimension as it will ultimately have when freed from the matrix.

One precaution, however, particularly applicable to laboratory specimens, should be mentioned. In some, just about to shed when preserved, a patchy or partly shed skin may be encountered, and when this is stripped from the specimen an additional rattle in the process of keratinization will be bared. This is likely to be shrunken and immature, and should be neglected in the accumulation of rattle statistics. Also, in captive specimens, segments acquired subsequent to captivity, particularly if the snake has failed to eat, may be smaller than those that had previously been acquired in the wild, and should be disregarded. Even when the captives feed regularly, their strings sometimes differ considerably from the normal strings found in wild snakes. This can be most easily verified when they have complete strings, so that their *W*-to-*N* relationships may be compared with those of wild snakes. Usually these captives have a greater number of rattles in the taper stage, as if the sheddings had been more frequent, relative to body growth, than is the case in the wild. This was quite evident, for example, in the previously mentioned captive-bred *atrox* raised by the late Mrs. Grace Olive Wiley at the Brookfield Zoo, in which the rattles somewhat resembled the gradually tapering strings pictured by the early natural-history writers. Other strings, similarly aberrant, in which each segment (except the button) was considerably smaller than the correspondingly numbered segment of the strings of wild rattlers, have been observed in captive specimens of *viridis* and *helleri*. Although these deviations from the normal are not universal, for some captive-raised snakes follow the wild trend quite closely, yet it is important not to place too much confidence in the reliability of data secured from the rattle dimensions of captive-raised snakes.

The first relationship that must be surveyed before the importance of species differences can be ascertained, is the consistency of rattle widths within homogeneous populations; for, obviously, if the rattle widths are highly variable and erratic within a group of snakes of one subspecies from a single area, species differences would be of doubtful importance.

A remarkable uniformity of the segment sizes has been found to exist within homogeneous populations. In a work of as wide a scope as this, it is necessary to condense statistical data, and I shall therefore merely summarize some of the conclusions regarding uniformity. The first investigation was devoted to the large homogeneous series that have furnished the basic data for my other statistical studies, including the Cape series of *lucasensis*, San Diego County *ruber*, Pierre

and Platteville *viridis*, Pateros *oreganus*, and San Diego County *helleri*. Necessarily, as the rattle-number of each segment had to be known, calculations were restricted to complete strings. Of these there were 3,172, comprising 10,468 measured segments. Many snakes were young-of-the-year, thus reducing the average number of segments per string.

With the sexes segregated—for some sexual dimorphism is apparent—the coefficient of variation in the width of the same segment in the several strings was found to range between 4 and 7½ per cent in most subspecies. Groups from areas of considerable ecological diversity—San Diego County *helleri*, particularly—had higher dispersions than those from more uniform localities. The dispersion of width in rattle No. 1 (the button) was usually about 1 per cent less than the dispersion in succeeding rattles, as if the exigencies of food supply and other conditions affecting the growing snakes had influenced the succeeding rattle sizes, especially during the period of most rapid growth, that is, in rattles Nos. 2 to 5.

The average variability of all the males (56 groups of segments, separately calculated) was found to be 6.10 per cent, and of the females 6.15 per cent. In order to visualize what these statistics mean, let us assume that the third segment of the rattle of male red diamonds averages 10 mm. in width. Then, with a coefficient of variability (the standard deviation divided by the mean) of 6.1 per cent, the widths of half the No. 3 rattles should fall between 9.6 and 10.4 mm., and 90 per cent of all the snakes would have No. 3 rattles measuring not less than 9.0 mm. nor more than 11.0 mm. Thus we see the considerable degree of consistency that is indicated by so low a coefficient of variation. The curve of dispersion was found to be substantially normal, although extreme deviants on the low side of the mean were more frequent than on the high. An example of the dispersion is given in table 5:4, setting forth the measurements of the buttons of the Platteville series of the prairie rattlesnake (*C. v. viridis*).

The question naturally arises as to what part of the dispersion in the width of any rattle is due to variations of snake size. This can best be investigated by consideration of the button, for, in this rattle, conditions that affect the chronology of shedding, which may involve factors other than mere size, have not yet become operative. The single-rattle young of the San Patricio series of western diamond rattlers (*C. atrox*), 71 males and 63 females, were investigated and it was found that the males had a coefficient of variation of 5.67 per cent, compared with a standard error of estimate of 5.48 per cent; the corresponding figures for the females were 5.31 and 4.33 per cent. The standard error of estimate should indicate the part of the rattle-width dispersion not attributable to the differences in the lengths of the young snakes, although this is not wholly true, as these young snakes were not preserved immediately after shedding the prebutton; thus they experienced some growth while the rattle widths remained constant. But the fact that there is some correlation—males,  $r = 55$  per cent; females,  $r = 48$  per cent—between body length and rattle size in these recently born young, indicates that individual size does affect rattle size slightly, a condition certainly to be expected. It should be pointed out that a much higher correlation was found to exist in specimens of the same species from diverse ecological niches, but in such a case the population is nonhomogeneous and therefore the result is of no interest in

connection with the particular problem at hand, namely, the correlation between the length of young snakes and the widths of their buttons in homogeneous populations. Ecological conditions undoubtedly affect both body and rattle sizes, as will be shown in the discussion of species differences.

I have mentioned the fact that, although the dispersion follows the normal probability curve, deviants from the segment-width mode are of occasional occurrence; they are of relatively greater frequency in the later than the early rattles,

TABLE 5:4  
WIDTHS OF RATTLE NO. 1 OF THE PLATTEVILLE SERIES OF *C. v. viridis*

Rattle width in tenths of a mm.	Number of snakes	
	Males	Females
45.....	1	..
46.....	..	1
47.....	2	2
48.....	3	2
49.....	8	6
50.....	9	7
51.....	21	14
52.....	51	40
53.....	56	35
54.....	69	51
55.....	36	55
56.....	55	58
57.....	48	28
58.....	20	26
59.....	12	10
60.....	9	5
61.....	4	6
62.....	..	2
63.....	..	2
64.....	1	..
65.....	..	1
Total.....	405	351

and are more likely to be below the mode than above. It is as if an extra shedding had been introduced, affecting some strings, and thus distorting the *W-N* relationship of all subsequent segments. In a previous publication (Klauber, 1945, p. 76) it has been shown that there is a correlation between successive rattle segments; snakes with some segments larger or smaller than normal size are likely to have others in the same category. The correlation between the button and rattle No. 2, was, however, found to be lower than that existing between subsequent pairs of adjacent segments. In conclusion, it should be said that, when comparisons are made between species, too much weight should not be given to the occasional string that deviates from the mode.

The second major problem of variability has to do with sexual dimorphism. It might logically be assumed that, as the males have thicker tails than the females of the same body size, the rattles, which are formed on the matrix terminating

the tail, should likewise be larger. This point was investigated by a tabulation of the average rattle width separately for each sex, in those species having sufficient measurements available from a limited geographical group to constitute what might be considered a reliable average for that group. Altogether, there were available for this part of the study, 10,711 measured segments from 3,161 snakes having complete strings.

The results indicate a slightly greater size of the rattles of the females, as compared to those of the males, in rattles Numbers 1 to 3 or 4 inclusive, the average dimensional difference being usually less than 2 per cent. This may be accounted for by the shorter and less-tapering tails of the females. However, in *oreganus*, *helleri*, and *laterorepens* the young males have a slight dimensional superiority of the same magnitude, that is, 2 per cent or less. In general, it can be said that, at least up to the fourth rattle, and in some species up to the sixth or seventh, sexual dimorphism is of relatively minor importance. Beyond this, as the snakes become fully adult, the greater size and the adult thickening of the tails of the males become more fully effective, and a difference becomes evident, the male superiority in rattle width reaching 5 per cent or more, at the tenth rattle or beyond. These average differences in the larger rattles usually cannot be determined with accuracy, since so few snakes retain complete strings of more than 10 rattles. The comparative increase in the male rattle widths is evident earlier in *oreganus* and *helleri* than in the other subspecies, becoming material at the fifth rattle, and this may also be true of some of the smaller rattlesnake species.

If a curve be drawn, for either sex of any homogeneous series of rattlesnakes, plotting the segment numbers as abscissas and rattle widths as ordinates, it will be found that the first few points—usually the first 4, but sometimes up to the first 6—fall almost exactly on a straight line. This means that there is a constant increase in width of each segment over its predecessor. The relationship is not exact, but where large numbers of specimens are available for validating averages, the regression closely approaches linearity. The second rattle is the one most frequently out of line, yet its deviation is not always in the same direction; in my 7 largest series it averaged slightly below expectation in 4 instances, and above in 3.

After the first 3 to 5 rattles, or 6 at most, the increments between successive widths decline materially, a decline that persists until finally there is no further increase in the widths of successive segments, and the rattle reaches the stage of virtual uniformity—a parallel rattle, as it may be termed.

This type of relationship—a straight line, followed by a drooping curve—is found to be characteristic of all rattlesnakes. The straight line, or constant increment, represents the period of rapid adolescent growth; it seems to terminate somewhat earlier—that is, at a lower rattle-number—in dwarfed subspecies such as island forms. It indicates, in a general way, that skin changes during this period are functions of size, that is, shedding takes place whenever the size increment has attained an appropriate figure, regardless of the time element, which latter is naturally affected by such conditions as hibernation and luck in securing food. It should be observed that a constant increment in measurement—say in millimeters—really represents a declining increment in terms of proportion of rattle size; for example, an increment of 1.5 mm. between a button measuring 5.0 mm.

and a No. 2 rattle 6.5 mm. in width, obviously represents a larger relative growth than a similar 1.5 mm. increment between rattles 4 and 5 measuring, respectively, 9.5 and 11.0 mm. This relationship is made clear in the following tabulation of the average percentage of growth of the successive segments of male red diamond (*C. r. ruber*) rattles:

	Incremental growth between segments						
	1 to 2	2 to 3	3 to 4	4 to 5	5 to 6	6 to 7	7 to 8
Per cent of button width.....	15	16	16	15	11	7	6
Per cent of width of first segment of each pair.	15	14	12	10	7	4	3

This declining proportional increment between widths of successive segments (particularly beyond the adolescent period) has an important adverse bearing on the possibility of accurately determining the rattle-number of the remaining segments of a broken string. As I have stated, this can be done with considerable accuracy if only the button is missing, or, at most, rattle No. 2 and the button. If only these are gone, one with experience can judge, by the shape of the distal rattle, how many that preceded it have been broken away and lost. And the measurements of the remaining segments will also be useful in allocating them, if they represent the straight-line period of rapid growth. But the proportion of segments that can be correctly placed declines rapidly beyond segment No. 2, since the increment between segment averages remains constant or declines, while the dispersion of the segment measurements tends to spread. It is easy to test this, as a practical matter, by experimenting with complete strings, disregarding the terminal 2 or 3 rattles as if they had been lost, and then trying to allocate the others by dimensions only. Or, in a large series, one may observe the number of No. 6 rattles falling within the normal range of Nos. 5 or 7. These ranges may be determined, either by tabulation of the frequencies of widths for successive segments, or by calculation.<sup>14</sup>

An investigation of the Platteville series of prairie rattlesnakes (*C. v. viridis*) showed a rapidly declining proportion of segments that could be properly allocated by width alone. The results were as follows, the first figure indicating the number of the segment under consideration, while the second, in parentheses, shows the percentage that would be properly allocated: 2(91.2), 3(85.7), 4(69.6), 5(51.6), 6(37.8), and 7(30.8). It will be seen how rapidly the chance of an accurate allocation declines, and how useless it is to try to guess how many segments are missing, when it is evident from the shape of the rattle that more than 2 or 3 are gone. And this, of course, presupposes the prior availability of large numbers of complete strings from the same subspecies of snake and from the same area, in order that the mean and dispersion of the successive rattle widths may have been established. Without such data the quest is hopeless, unless dependence be placed entirely on the shape of the oldest remaining segment, and this requires experience for a decision. We cannot agree with Bosc (1803, vol. 6, p. 551; Griffith and Pidgeon, 1831, p. 336), who thought the increase in the sizes of successive segments to be so regular that one could always tell, by calculation, how many were missing.

<sup>14</sup> The formula for this equal probability division between successive segments is  $P = (M_1\sigma_2 + M_2\sigma_1)/(\sigma_1 + \sigma_2)$ , where  $M$  and  $\sigma$  represent the means and standard deviations of the widths of the successive segments.

In a special study of the Cape series of *lucasensis*, I was able to allocate rattle strings with considerable accuracy with as many as 3 or 4 segments missing. This is a subspecies characterized by large rattles and large increments in width up to the sixth segment. Good series of complete strings, together with a number of broken strings in the taper stage, enabled me to place the latter with considerable assurance, so that I was able to build up hypothetical rattle strings and establish the average *W-N* and *L-N* relationships up to rattle No. 14, and even beyond (table 5:5; see also figs. 5:18 and 5:19).

TABLE 5:5  
WIDTHS OF SUCCESSIVE RATTLES IN SAN LUCAN DIAMONDBACKS—ALSO BODY LENGTHS  
OVER-ALL AT ACQUISITION OF EACH RATTLE

Rattle number	Average rattle width		Average body growth while each rattle is the proximal rattle		Increment in rattle width over prior rattle		Body growth prior to acquisition of next rattle	
	Males	Females	Males	Females	Males	Females	Males	Females
1....	7.50	7.76	328- 436	333- 441	....	....	108	108
2....	9.19	9.37	436- 536	441- 538	1.63	1.61	100	97
3....	10.72	10.84	536- 621	538- 625	1.53	1.47	85	87
4....	12.06	12.25	621- 715	625- 721	1.34	1.41	94	96
5....	13.37	13.58	715- 822	721- 819	1.31	1.33	107	98
6....	14.58	14.60	822- 915	819- 895	1.21	1.02	93	76
7....	15.37	15.02	915- 975	895- 933	0.79	0.42	60	38
8....	15.87	15.30	975-1,017	933- 955	0.50	0.28	42	22
9....	16.22	15.45	1,017-1,046	955- 970	0.35	0.15	29	15
10....	16.48	15.57	1,046-1,069	970- 981	0.26	0.12	23	11
11....	16.70	15.65	1,069-1,089	981- 989	0.22	0.08	20	8
12....	16.88	15.71	1,089-1,105	989- 995	0.18	0.06	16	6
13....	17.02	15.76	1,105-1,117	995-1,000	0.14	0.05	12	5
14....	17.10	15.80	1,117-1,127	1,000-1,004	0.08	0.04	10	4

Note.—All dimensions in millimeters; larger rattles were computed from studies of incomplete strings.

Just where the increment between successive rattle segments falls to zero and the string becomes parallel, I do not know; the investigation of the *lucasensis* series indicates that it falls practically to zero at segment 15 in the females and a little later in the males, possibly at 18. This is closely connected with the problem of whether adult snakes grow continuously, although more and more slowly, all their lives. Studies of captives, to whatever extent such studies may be considered valid, indicate that they do not grow until death. At any rate, an investigation of long broken strings on wild rattlers shows clearly that the rattle-width increment eventually does fall to zero; and long before this happens the increment is completely masked by fluctuations in width, up to 5 per cent on either side of the mean. I have looked for regular cycles in these long parallel strings, hoping that some regularity might coincide with a certain season of each year—an especially large rattle acquired in spring, for example—but I have failed to discover any. As one notes the fluctuations of segment size in such wild rattlers as come in with long parallel strings—fluctuations, not only in the width *W* that has been the basis of this discussion, but in other dimensions as well—one cannot but speculate as to what conditions of food supply, hibernation, forest fires, illness, and the

other events in the life of the creature may have so affected the dimensions of the rattle matrix, and therefore of the rattle formed on it. In adult captive specimens, reductions in rattle size after captivity are often very noticeable, amounting in some cases to 10 per cent; and one may presume that the misfortunes of old age must cause similar reductions in the wild.

Before concluding the discussion of rattle width, we should make mention of the prebutton, the rattle with which every young snake is born, but which, unlike the true button, is shed and lost with the young snake's first change of skin a week or so after birth. If the prebutton is to be conserved, the young snakes must be preserved within this short interval. For this reason, almost no wild snakes with prebuttons are available in preserved collections, and we are dependent for data on captive-born young, which are not always normal. Measurements derived from unborn embryos must be avoided, and the specimen catalogues do not always state whether the young were born alive. The most authoritative data I have on prebuttons represent the measurements of the prebuttons of 73 young prairie rattlers (*C. v. viridis*) from Montana, whose mothers were captured only a short time before the young were born. The average prebutton width was 4.69 mm. The average of 68 Montana buttons was 5.25 mm., and, of 59 No. 2 rattles, 6.36 mm. Thus, the increment between the prebutton and the button was 0.56 mm., compared with 1.11 mm. between the next two segments (the increment between Nos. 2 and 3 was 1.06 mm.), and it is evident that the prebutton does not fall on the straight line that characterizes the dimensional relationship of the succeeding 3 to 5 rattles of all species.

In a brood of 11 San Diego County *C. v. helleri*, born a few days after the mother was captured, the prebuttons varied in width from 5.4 to 6.1 mm., with a mean of 5.72 mm. In a large series of *helleri* from the same area, the average widths were: button, 6.73 mm.; No. 2 rattle, 8.18 mm.; No. 3 rattle, 9.69 mm. Thus we find the increments in width to be: prebutton to button, 1.01 mm.; button to No. 2 rattle 1.45 mm.; No. 2 to No. 3 rattle, 1.51 mm.; and again we note, as in the Montana series, that the prebutton is larger than expected, if it were presumed to fall on the regression line representing the widths of the succeeding rattles.

As previously stated, there are three variables whose interrelations may be investigated in connection with rattle dimensions; these are segment width ( $W$ ), the serial number of the segment in the string ( $N$ ), which is known with certainty only if the string is complete, and the length of the snake over-all ( $L$ ). The  $W$ - $N$  relationship has already been discussed rather fully; I shall now mention the  $N$ - $L$  and  $W$ - $L$  correlations, but shall do little more than summarize the conclusions reached in an unpublished study.

The  $N$ - $L$  relationship is, like the  $W$ - $N$ , available only when the string is complete, and hence only a limited proportion of the snakes in a collection supply pertinent data. Theoretically, the curve is not a smooth one, but comprises a series of steps (fig. 5:19), for  $N$  remains constant between sheddings, while  $L$  increases continuously as the snake grows. Thus, a true  $N$ - $L$  curve would be a series of alternating horizontal and vertical lines between two curves, one of which would represent the  $N$ - $L$  relationship just prior to each shedding, the other immediately after, when the next rattle had been exposed. These true curves cannot be deter-

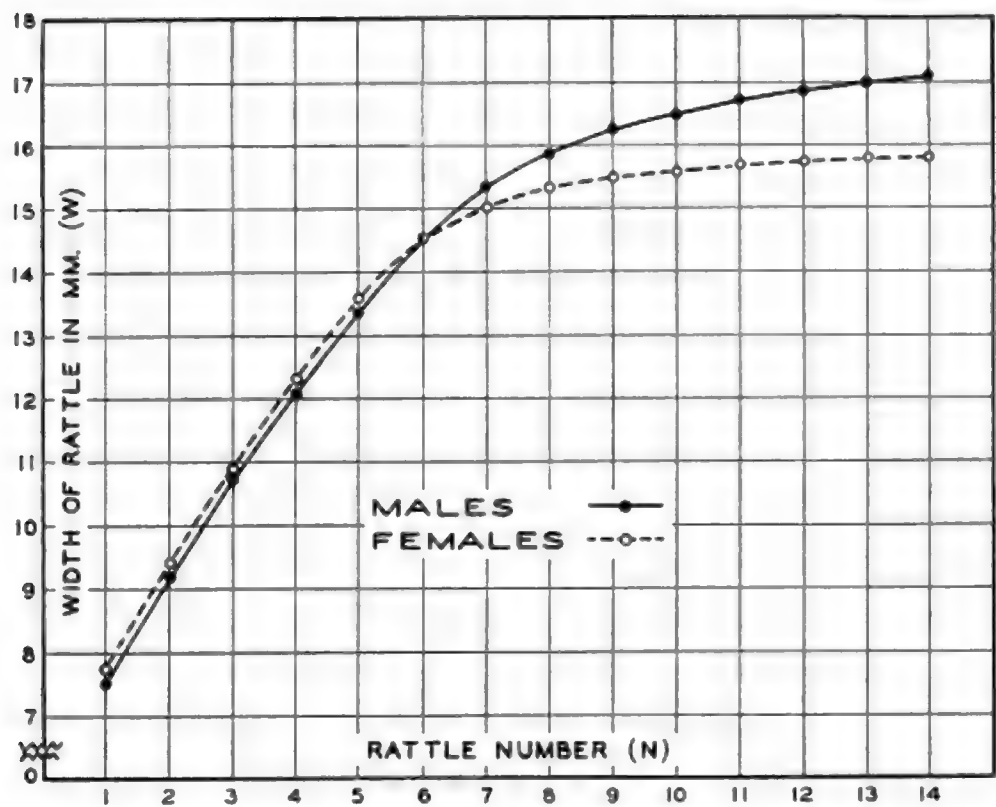


Fig. 5:18. Relationship between any segment number and the width of its anterior lobe in typical rattle-strings of the San Lucan diamondback (*C. r. lucasensis*).

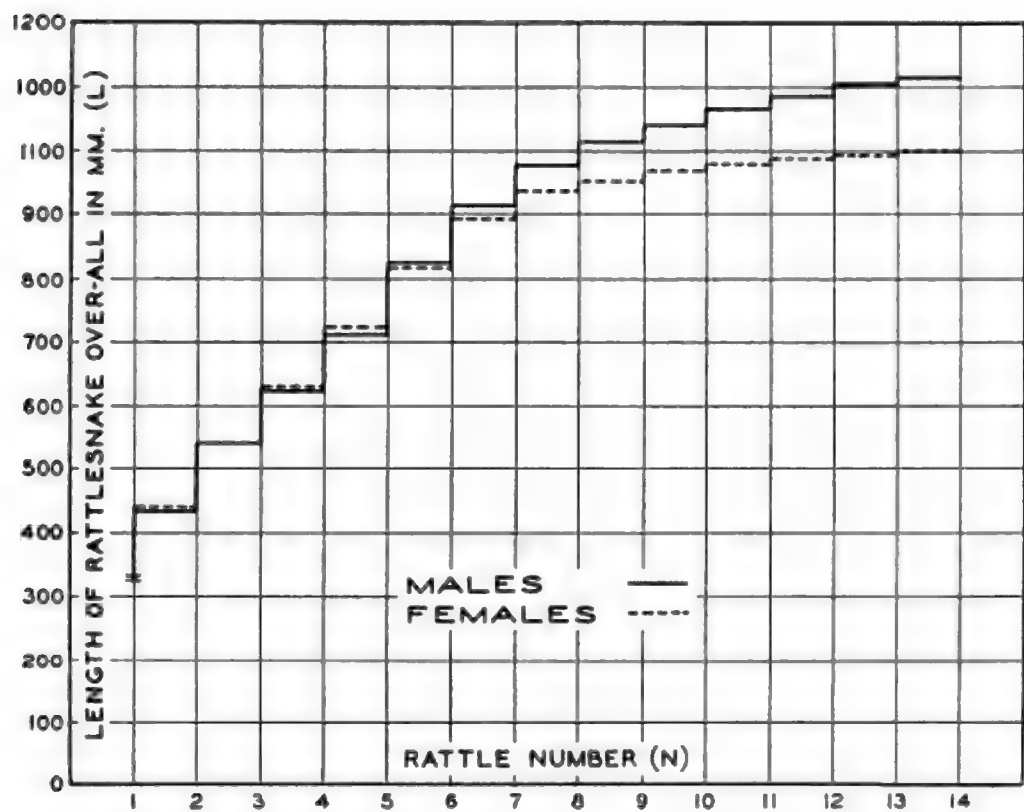


Fig. 5:19. Relationship between a segment number and the over-all length of the rattlesnake, when that segment is the proximal one, in typical rattle-strings of the San Lucan diamondback (*C. r. lucasensis*)

mined with accuracy, but a study of a large number of specimens, which will give the average *L* between each pair of sheddings, may be taken as indicating the average *N-L* relationship, a correlation already mentioned under growth (p. 301). The following additional points summarize the conclusions respecting the *N-L* curve: For any given rattle number, there is practically no sexual difference in the average body length when the snakes are young, that is, up to rattle No. 6 or 7. Beyond this the males have longer bodies for any rattle number, reaching 10 per cent longer at the eighth rattle or beyond. This adult difference may be interpreted in one of two ways: either the females shed more frequently, or the

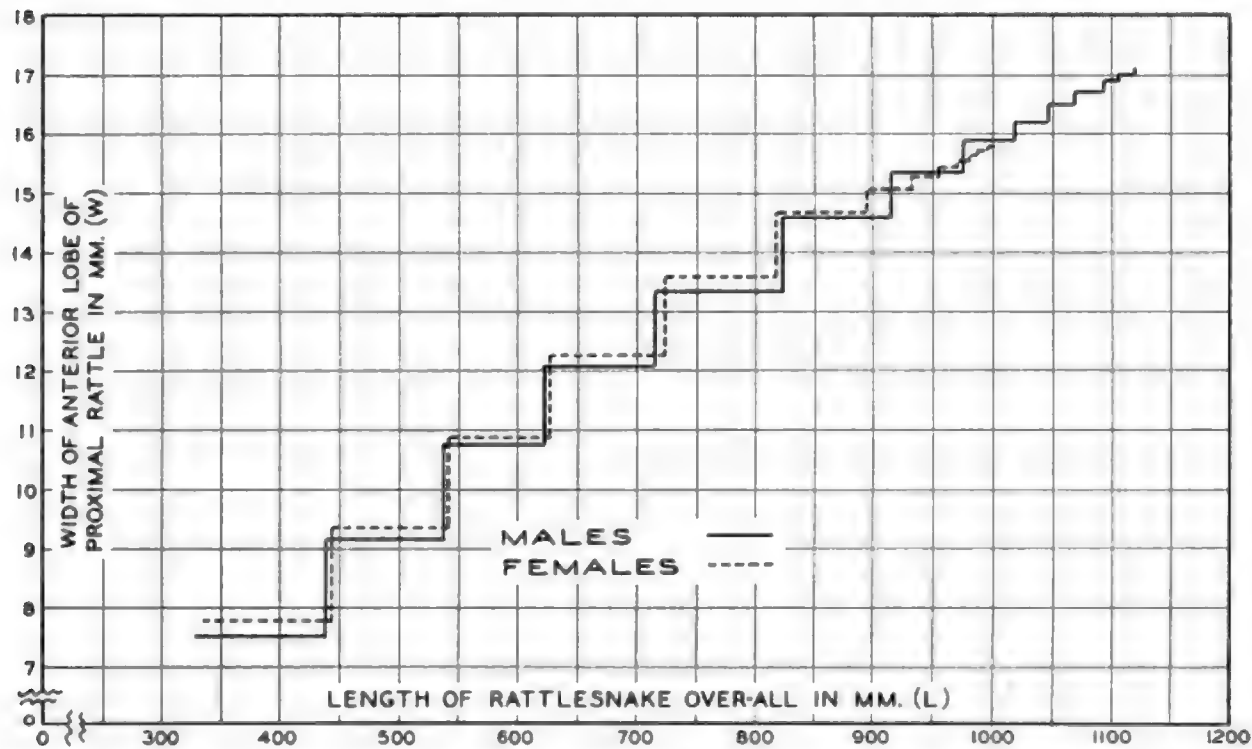


Fig. 5:20. Relationship between the over-all length of the rattlesnake and the width of anterior lobe of its proximal rattle in typical rattle-strings of the San Lucan diamondback (*C. r. lucasensis*).

males grow faster between sheddings. (The latter presumption is substantiated by other considerations.) In each species there is a fairly constant body-length increment (the relationship is not exactly linear), as each rattle is added, up to the fifth to seventh rattle; beyond this the increments of body length between rattle additions are reduced. Thus it is again indicated that skin changes are first correlated with body growth, but later are required because of some other condition, probably wear, a conclusion reached before, upon other data.

In considering the *W-L* relationship, it is to be remembered that only the attached, or proximal, rattle furnishes data; thus there is but one figure per snake, but every specimen supplies such a figure even though the string be incomplete. I have had available in this investigation well over 12,000 rattlesnakes of which the proximal rattles were measured.

The *W-L* curve, like the *N-L*, is a step-type curve (fig. 5:20), for *W* remains constant between sheddings while *L* is continuously increasing. But, in this curve, both the treads and risers gradually decrease in size; for, as the sheddings come at intervals of lesser body growth, so also do the rattle-width increments decrease with each new segment.

The average  $W$ - $L$  curve, representing the mid-points of the steps and risers, was investigated in a number of species, with the following conclusions: In rattlesnakes of equal lengths, juvenile females have slightly larger proximal rattles than males; but the contrary is true in the adults of most species, the males having larger proximal rattles than females of the same length. Eventually, as the males attain a greater size than the females (except in sidewinders) the male rattles reach a greater width than those of the females.

In each species, there is an approach toward a linear correlation between body length and attached rattle width up to rattle No. 4 or 5, or during the first year of life, after which the curve falls off slightly, with decreasing increments of  $W$  for constant increments of  $L$ . In other words, adult snakes have proportionately somewhat smaller proximal rattles (as measured by the width of the exposed lobe) than juveniles. For example, in male prairie rattlesnakes (the Platteville series) the width of the button averages 1.8 per cent of the over-all length of the snake at birth, whereas in a 900-mm. adult the width of the proximal rattle is about 1.5 per cent of the length. Even with respect to the first 6 rattles, the regression is not exactly linear, for there is a slight reverse curvature, the increments in rattle width, per unit body increment, being higher at rattles Nos. 3 and 4 than at Nos. 1 and 2, or 5 and 6. Of course, this single size criterion (width) overlooks the fact that the button is much shorter, with only 2 ill-defined lobes, while the mature segment comprises 3 well-defined lobes and is correspondingly both longer and thicker than the button.

From the correlations between rattle number, rattle width, and snake length that have been investigated, and assigning incomplete strings in accordance with the principles of maximum likelihood, I have devised, for the Cape series of *C. r. lucasensis*, the complete data required to plot the  $W$ - $N$  point curve, and the  $L$ - $N$  and  $L$ - $W$  step curves, up to and including rattle segment No. 14 for both sexes. The actual points as determined by the measurements and calculations have been somewhat emended to secure regular curves, yet I have little doubt that these idealized data closely approximate the average rattle relationships. The data are set forth in table 5:5. While the dimensions here given are applicable only to a single subspecies of rattlesnake, they illustrate the type of growth characteristic of all rattlers. The relationships are also shown graphically in figures 5:18 to 5:20.

#### SPECIES DIFFERENCES IN RATTLES

Having discussed the basic features of the dimensional relations between successive rattles, and between the rattle and the length of the snake, we are now prepared to assess the importance of species differences in these rattle proportionalities.

Naturally it would be expected that rattle sizes would vary with the sizes of the snakes to which they are attached, and that a fairly constant ratio might be presumed to exist between them. But although it is true that larger species have larger rattles,<sup>15</sup> and that, as each individual snake grows, the segments of its rattles become successively larger, the ratio of the width of the proximal rattle to the length of the snake is by no means constant throughout the rattlesnake genera. On the contrary, some species have unusually large rattles, when judged by their

<sup>15</sup> Mauduyt (p. 387) noted the difference between *atricaudatus* and *miliarius* rattles as early as 1774.

body lengths, whereas those of others are notably small, and these differences are found to be consistent with species relationships that have been verified by other characters. Furthermore, there are ontogenetic differences between species—that is, changes in the rattle-body ratios as the snakes age; for one kind of rattler may start with a button inconsistently small for its body size at birth, yet the successive segments may increase by such large steps that eventually it has larger rattles, proportional to body length, than another species that started with a larger button. It is with these differences in rattle sizes and growth trends that I shall now deal.

Some of the early rattlesnake classifications employed the shape of the rattle string as a key character, segregating the acuminate from the parallelogrammic (Cope, 1866, p. 308). Later this was abandoned when it was observed that a parallelogrammic rattle was merely an adult string from which the acuminate, or youthful, section had been lost through breakage or wear (Cope in Yarrow, 1875, p. 533; Garman, 1887, p. 2).<sup>16</sup> But even so, the rattle should not be entirely overlooked as a significant species difference or a possible key character; especially is it useful where large numbers of specimens are available for the determination of average dimensions.

We may first survey species differences by comparing the widths of correspondingly numbered rattle segments of the several species, thus, for the moment, making no attempt to fix a definite ratio with body size. We find that *C. m. mitchelli* from the Cape Region of Baja California, has the largest rattles, at least up to the fourth rattle; that is, each rattle exceeds in width the same rattle of any other kind of rattlesnake. This is surprising, since this is not a particularly large species. Following *mitchelli* in absolute size of rattles, we have, in order, *lucasensis*, *adamanteus*, and *atricaudatus*. It is of interest to observe that the two outstanding subspecies are found only in the southern half of the peninsula of Baja California. The other two both grow to a very large size.

These remarks apply to the rattles during the period of most rapid growth, that is, up to the fourth or fifth rattle. It would seem, therefore, that a climatic condition involving a short period of winter inactivity tends to produce large rattles, for this seems the only condition common to these Pacific Coast forms. It will be noted that, even within a species, body size is not the sole factor controlling rattle size, for *C. m. mitchelli* from the Cape Region of Baja California is a smaller snake, on the average, than San Diego County *C. m. pyrrhus*, yet it has larger rattles. *C. r. lucasensis* is about the same size or slightly smaller than *C. r. ruber*, but has distinctly larger rattles; and both exceed, in rattle size, their relative, *atrox*, a larger snake. Beyond the fifth rattle mere body size becomes effective; *mitchelli* quickly loses in the race for supremacy; it is passed by *lucasensis* and *adamanteus*, and eventually by several other large species.

At the opposite extreme are the snakes having the smallest rattles. These are the pigmy rattlers (*Sistrurus miliarius* and its subspecies), and, in the genus *Cro-*

<sup>16</sup> This difference between pointed and parallel strings had also been presumed, erroneously, to be a sexual difference, the pointed strings were allegedly found on the males and the blunt on the females. Sometimes the reverse was believed to be true (Adair and Ewhank, 1922, p. 356), and the females were presumed to have the more tapered rattles, which, incidentally, were thought to produce a shriller note. This myth is still occasionally heard in the Southwest. It is akin to the equally mistaken idea that the males carry their rattles with the flat side vertical, whereas the females have the flat side horizontal, as Burton (1869, vol. 2, p. 181) was told in Brazil. This remains a fruitful source of discussion in the queries columns of sportsmen's magazines.

*talus*, the Tancitaran dusky rattlesnake (*C. pusillus*), the central-plateau dusky rattlesnake (*C. t. triseriatus*), and the long-tailed rattler (*C. stejnegeri*).

But these last are notably small snakes, just as the eastern diamondback (*C. adamanteus*) is especially large, which suggests that some basis of comparison should be devised that will take body size into consideration, such as the comparison of the rattles of rattlesnakes of similar ages. One of the stages of rattlesnake life, at which average body size can be established with a moderate degree of accuracy, is the size at birth; and correspondingly we have available for most kinds of rattlers the width measurements of many buttons. When we plot on a scatter diagram the points determined by the average lengths at birth (table 4:1) as abscissas and the average button widths as ordinates (one point for each subspecies), a pattern of relationship is immediately evident, for most of the points fall within a band, the center line of which is represented approximately by the parabola  $W = -118.21L^2 + 91.50L - 9.79$ , where  $W$  is the width of the button in millimeters and  $L$  is the snake length in meters. This formula indicates that smaller rattlesnakes have proportionately smaller buttons, or No. 1 rattles, than the larger species; for example, a species 170 mm. long at birth would have a button 2.3 mm. wide, whereas a species 320 mm. long would have one 7.4 mm. wide. The ratio of rattle width to body length in the two cases is 1.35 and 2.31 per cent, respectively. As the largest rattlesnakes (*adamanteus*) measure about 350 mm. at birth, the formula is inapplicable above  $L = 0.35$ .

Most of the species and subspecies fall within 15 per cent of the parabolic line whose equation I have given, but a few deviate more widely. *C. m. mitchelli* and *C. tigris* have conspicuously large buttons. As I have already stated, *mitchelli* is outstanding; for, although it is of moderate size, normally attaining an adult length of about 940 mm. (37 in.), it has the widest button of all rattlesnakes, slightly wider, indeed, than the button of the largest of all rattlesnakes, the eastern diamondback (*C. adamanteus*), which occasionally exceeds 1,830 mm. (6 ft.) in length. In the other direction, subnormally small buttons are found on *durissus*, and its subspecies, and on *unicolor*, *basiliscus*, *polystictus*, and *pusillus*. *C. d. durissus* and *C. b. basiliscus* are large rattlesnakes, exceeded in ultimate size only by *adamanteus*, *atrox*, and possibly *atricaudatus*; yet their buttons are little more than  $\frac{1}{2}$  the width—which means about  $\frac{1}{8}$  the bulk—of *adamanteus* buttons.

Island and other dwarfed derivatives have proportionately larger buttons than their prototypes; falling in this category are *tortugensis* (*atrox*), *exsul* (*ruber*), *nuntius* (*viridis*), *caliginis* (*helleri*), and *muertensis* (*mitchelli*), the ancestral forms being shown in parentheses. This does not mean that the stunted rattler actually has a larger button than its relative, but that it is larger proportionate to the snake's length, a fact long ago noted by Garman (1888, p. 263).

Other differences of interest are these: *C. atrox* in Texas has a smaller button than the same species in Arizona and California, although the Texas snakes reach a larger size than those farther west; and *lucasensis* has a larger button than *ruber*, although the latter snake probably attains a slightly greater ultimate length. Large buttons are characteristic of the snakes of the extreme Southwest.

The smallest of all buttons (both proportionately and actually) are those of *Sistrurus miliarius streckeri* and *Crotalus pusillus*, which average about 1.6 mm. Both are small snakes, so that small rattles would be expected; however, they are

also long-tailed, compared with other rattlers, which no doubt further explains the small size of their diminutive rattles, since a small matrix would be appropriate to the end of a long, tapering tail. The long tail also explains, at least in part, the relatively small button of *durissus* and its allies.

There is no adult length capable of being fixed quite so objectively as that of the size at birth; however, from a study of available material I have arrived at the probable lengths of what may be termed large, but not exceptional, males of each subspecies (table 4:1), and have used these in other statistical studies (1937, p. 28; 1952, p. 128). Using these lengths, I have determined, from *L-W* curves drawn for each subspecies, the average width of the proximal rattle at that body length. Again, these measurements, large-male length and corresponding rattle width, have been plotted as a scatter diagram, each subspecies (or homogeneous series) being represented by a single point. It may be noted that, even if the best judgment has not been used in fixing the standard adult male length, no considerable inaccuracy results, since the corresponding width of the proximal rattle has been appropriately modified by use of the *L-W* curve.

This relationship, also, is found to follow a parabolic curve, its equation being approximately  $W = -7.16L^2 + 30.96L - 9.51$ , with *W* expressed in millimeters and *L* in meters. Again there is an increase in the rattle proportionality from the small to the large species, although not so marked as in the formula for the buttons. A small species with a length of 600 mm. (representing a large male of that species) would have a proximal rattle width of 6.5 mm. (1.08 per cent of the body length), whereas a 1,500-mm. species would have a 20.8 mm. rattle (1.39 per cent). These are the widths at which the strings become parallel or uniform in size.

As before, there are some conspicuous deviations from the generic trend or regression line. The largest rattles, proportionate to the adult body lengths, are possessed by *lepidus*, *tigris*, *mittelli*, *cerberus*, *pyrrhus*, and *nigrescens*. The snakes having notably small rattles are again the long-tailed forms, *stejnegeri*, *miliarius* (and its subspecies), *pusillus*, *triseriatus*, and *polystictus*. *C. d. durissus* and the others of that group, although starting with small buttons, have, by rapid increments in the widths of their succeeding segments, been brought above the rattle-snake mode. The eastern rattlers *adamanteus*, *horridus*, and *atricaudatus* are all on the low side of the regression line, although they do not deviate conspicuously from the mode. *C. r. ruber*, as an adult, also has a relatively small rattle. All *Sistrurus* forms are low, but the others are not so low, proportionately, as *miliarius*. *C. lepidus* and its subspecies have conspicuously larger rattles than *triseriatus* and its relatives, especially *t. triseriatus*, which has a strikingly smaller rattle than *t. aquilus*.

One interesting conclusion from this relationship is that the island forms, and other stunted races that had larger than modal buttons, to some extent lose this superiority as they age. It seems evident that the ecological conditions that cause dwarfing are increasingly effective postnatally, a trend previously verified in other characters.

The smallest of all adult rattles are those of *stejnegeri*, *pusillus*, and *miliarius* and its subspecies, which reach parallelism at widths of 3.3 to 4.0 mm. The largest rattles are those of *atrox*, *culminatus*, *tzabcan*, *durissus*, and *basiliscus*, which average about 22.0 mm. in the biggest males, although less in the usual run of adults.

Some exceptionally large strings have been seen on *basiliscus* and *atrox*; I have measured parallel strings on the former up to 24.3 mm. in width and 24.7 mm. on the latter.

Rattlesnakes not only follow trends that indicate relationships in the relative sizes of their rattles, but also in the increments in width between successive segments during the adolescent stage wherein these increments are substantially constant. For example, expressed as percentages of the button widths, the average increments between the first 4 rattles in the related forms *durissus*, *culminatus*, *terrificus*, *basiliscus*, and *enyo* are, respectively, 30.2, 36.2, 31.8, 36.2, and 36.6 per cent; whereas in the *atrox* group of *atrox*, *ruber*, *lucasensis*, *exsul*, and *tortugensis* they are 18.8, 14.7, 19.5, 13.3, and 16.9 per cent. Another consistent group is composed of *mittelli* (18.3), *pyrrhus* (16.4), *muertensis* (15.5), and *tigris* (13.9). From these, *stephensi* (25.5) differs materially. In these increment ratios, island and other dwarfed forms are usually found to be lower than their ancestral prototypes; for, as I had previously noted, the buttons are generally larger than are to be expected in snakes of their size, but the subsequent rattles are less extreme, as if stunting were increasingly effective with age.

The consistency of these incremental trends suggests their use in verifying relationships. For example, *cerastes* has a high ratio, which suggests an affinity to the *durissus* group, as is further indicated by the rugosities on the dorsal scales. The variations of rattle size between species cannot be explained by any differences in use. The rattles of the western diamond (*C. atrox*) increase in width, relative to body size, from Texas west to Arizona and California, yet the snakes from the latter area would seem to have no reason to use their rattles more often; nor should they be subjected to greater wear.

In separate geographical populations that do not warrant subspecific recognition, there is a considerable consistency in the widths of the corresponding rattles. The following figures show the average width of each rattle of several series of *viridis* and one of *nuntius* as a percentage of the width of the same segments in South Dakota *viridis*, the latter, the largest, as well as the most northeasterly group, being taken as 100 per cent:

	Rattle-number				
	1	2	3	4	5
South Dakota <i>viridis</i> . . . . .	100.0	100.0	100.0	100.0	100.0
Colorado <i>viridis</i> . . . . .	92.1	91.2	90.9	90.9	90.6
New Mexico <i>viridis</i> . . . . .	91.8	87.9	85.4	83.7	86.0
Arizona <i>nuntius</i> . . . . .	77.9	75.8	73.8	72.1	68.4

Again we observe the gradually declining relative rattle-size in each geographical series that characterizes the tendency of dwarfed forms to widen their differences from their prototypes with increasing age. The same condition is found true of desert-slope *ruber*, as compared with its larger coastal relative.

When one has a sample population of snakes to be compared with another, and specimens of known age criteria—such as young just after birth, or gravid females with their first broods—are not available, complete rattle strings, since they are, in a way, preserved bench marks, sometimes will aid in solving a problem of relationship. For example, I have heard it stated that the southern Pacific rattlesnakes

(*C. v. helleri*)<sup>17</sup> on Santa Catalina Island, California, were probably recently introduced, having been accidentally transported there with plants for gardens. But a small series of Catalina rattlers with complete rattle strings have the following widths, expressed as percentages of mainland *helleri* for the first 4 rattle segments: 78.2, 79.2, 75.9, 75.0. There were not available from the island sufficient specimens to make sure that they differ conspicuously in average body size from those on the mainland, but the rattles indicate that they do; and it is certainly not probable that dwarfing to this degree could have occurred in so short a time. We may conclude that they are not a recent importation.

Sometimes rattle dimensions may be useful in verifying identifications, where a specimen is poorly preserved, or has an aberrant pattern. For example, the first two rattles of *basiliscus* average 4.7 and 6.4 mm. in width, respectively, while the corresponding figures for *molossus* are 6.9 and 7.9. These considerable differences will aid materially in identifying specimens of these two occasionally confused species, if the rattle string of the doubtful individual is complete. Beyond the second rattle, the differences decline, for *basiliscus* gradually overtakes *molossus* in rattle size, being slightly larger at the fifth rattle and conspicuously so at the sixth. The differences in the rattle dimensions of *C. t. triseriatus* and *C. t. aquilus* are of sufficient magnitude to be important in segregating specimens of these two subspecies, which, otherwise, are much alike in most characters.

Thus far I have discussed the general *W-L* relationships in the two genera of rattlesnakes, but have presented little dimensional information applicable to particular species. With regard to the widths of the button and the next 3 to 5 rattles, I have pointed out that there is a constancy in the increment of the width of each segment over its predecessor. Therefore, given the average width of the button of any subspecies, and the average increment, one may determine, with an error that generally will not exceed 10 per cent, the widths of the first 4 to 6 rattles of a complete string. The data necessary for these determinations are set forth in table 5:6.

The presentation of similar data for adults is less simple because of an increased importance of sexual dimorphism, and a widening dispersion about the mean. It is no longer possible to present the dimensions of a particular segment in the sequence of rattles, since the sequence number is so seldom known, because of the almost invariable loss of an unknown number of rattles from any adult string. As the adult rattles are (within each subspecies) affected by the size of the snake itself, we are reduced to recording *W*, the width of the proximal, or attached, segment in terms of *L*, the length of the snake over-all. I have already pointed out that the *W-L* regression line is not exactly linear, although reasonably useful approximations to the curve can be given in this form, as, for example:

<i>C. b. basiliscus</i>	$W = 0.013L + 0.60$	<i>C. m. molossus</i>	$W = 0.014L + 1.25$
<i>C. d. durissus</i>	$W = 0.014L - 0.54$	<i>C. p. pricei</i>	$W = 0.012L + 0.06$
<i>C. d. culminatus</i>	$W = 0.015L - 1.00$	<i>C. pusillus</i>	$W = 0.0058L + 0.30$
<i>C. l. klauberi</i>	$W = 0.015L + 0.48$	<i>C. t. triseriatus</i>	$W = 0.007L + 0.60$

But data in this form are not useful to some readers, and more accurate parabolic curves would be even more cumbersome. It appears appropriate, therefore, to present the data applicable to adult rattlers in the form of their *W/L* ratios,

<sup>17</sup> Not to be confused with the Santa Catalina Island rattlesnake (*C. catalinensis*) on Santa Catalina Island in the Gulf of California, Mexico.

TABLE 5:6  
AVERAGE RATTLE DIMENSIONS AND RATIOS

Subspecies	Juvenile and adolescent rattles				Adult rattle
	Width of button, mm.	Succeeding increments between segments for the next 3 or 4 segments, mm.	Ratio, increment to button, per cent	Ratio, button to length at birth, per cent	Ratio W/L, per cent
<i>C. adamantus</i>	8.1	1.2	14.8	2.31	1.18
<i>C. atrox</i>	6.9	1.3	18.8	2.09	1.62
<i>C. basiliscus basiliscus</i>	4.7	1.7	36.2	1.42	1.36
<i>oaxacus</i>	5.7	1.0	17.5	...	1.78
<i>C. cerastes cerastes</i>	3.0	0.9	30.0	1.71	1.45
<i>cercobombus</i>	3.3	1.1	33.3	1.78	1.58
<i>laterorepens</i>	3.4	1.0	29.4	1.79	1.49
<i>C. durissus durissus</i>	4.3	1.3	30.2	1.36	1.33
<i>culminatus</i>	4.8	1.7	36.2	1.57	1.46
<i>terrificus</i>	4.4	1.4	31.8	1.44	1.39
<i>totonacus</i>	4.8	1.6	33.3	1.57	1.17
<i>tzabcan</i>	4.6	1.4	30.5	1.46	1.34
<i>C. enyo enyo</i>	4.1	1.5	36.6	1.82	1.67
<i>C. ersul</i>	6.0	0.8	13.3	2.50	1.45
<i>C. horridus horridus</i>	6.2	1.3	21.0	2.18	1.43
<i>atricaudatus</i>	7.0	1.6	22.9	2.34	1.38
<i>C. intermedius intermedius</i>	2.8	0.5	17.8	1.87	1.27
<i>gloydi</i>	2.6	0.4	15.3	1.73	1.12
<i>omiltemanus</i>	2.5	0.5	20.0	1.56	1.10
<i>C. lepidus lepidus</i>	3.9	0.9	23.1	2.05	1.67
<i>klauberi</i>	3.5	0.8	22.8	1.79	1.60
<i>morulus</i>	2.6	0.4	15.4	1.37	1.05
<i>C. mitchellii mitchellii</i>	8.2	1.5	18.3	3.42	1.78
<i>angelensis</i>	5.2	1.1	21.2	1.96	1.15
<i>muertensis</i>	5.8	0.9	15.5	3.14	1.72
<i>pyrrhus</i>	6.7	1.1	16.4	2.58	1.76
<i>stephensi</i>	5.1	1.3	25.5	2.22	1.53
<i>C. molossus molossus</i>	6.9	1.0	14.5	2.46	1.53
<i>nigrescens</i>	6.3	1.2	19.0	2.34	1.56
<i>C. polystictus</i>	3.6	0.6	16.7	1.57	1.06
<i>C. pricei pricei</i>	2.6	0.4	15.4	1.62	1.22
<i>C. pusillus</i>	1.6	0.2	12.5	0.91	0.65
<i>C. ruber ruber</i>	7.5	1.1	14.7	2.50	1.36
<i>lucasensis</i>	7.7	1.5	19.5	2.66	1.53
<i>C. scutulatus scutulatus</i>	5.7	1.0	17.5	2.15	1.50
<i>salvini</i>	...	...	...	...	1.55
<i>C. stejnegeri</i>	2.1	0.3	14.3	1.23	0.51
<i>C. trigris</i>	7.2	1.0	13.9	3.43	1.73
<i>C. tortugensis</i>	6.5	1.1	16.9	2.60	1.38
<i>C. transversus</i>	...	...	...	...	1.16
<i>C. triseriatus triseriatus</i>	2.0	0.3	15.0	1.14	0.82
<i>aquilus</i>	2.9	0.5	17.2	1.66	1.20
<i>C. unicolor</i>	3.4	...	...	1.45	1.43
<i>C. viridis viridis</i>	5.3	1.1	20.8	1.96	1.43
<i>abyssus</i>	5.3	1.0	18.8	2.12	1.45
<i>caliginis</i>	6.1	0.9	14.8	3.21	1.78
<i>cerberus</i>	6.0	1.2	20.0	2.35	1.69
<i>concolor</i>	4.1	0.7	17.1	2.00	1.42
<i>helleri</i>	6.7	1.5	22.4	2.44	1.63
<i>lulosus</i>	5.6	1.1	19.7	2.11	1.44
<i>nuntius</i>	4.3	0.8	18.6	2.39	1.54
<i>oregonus</i>	5.7	1.0	17.5	2.11	1.60
<i>C. willardi willardi</i>	2.2	...	14.1	1.33	1.24
<i>amabilis</i>	...	...	...	...	1.18
<i>meridionalis</i>	...	...	...	...	1.12
<i>silus</i>	2.4	...	...	1.41	1.17
<i>S. catenatus catenatus</i>	3.5	0.9	25.7	1.59	1.27
<i>tergeminus</i>	3.3	1.0	30.3	1.54	1.25
<i>S. miliarius miliarius</i>	...	...	...	...	0.70
<i>barbouri</i>	1.9	0.3	15.8	1.12	0.65
<i>streckeri</i>	1.6	0.4	25.0	0.92	0.62
<i>S. rarus</i>	2.3	...	...	1.31	0.98

as set forth in the final column of table 5:6. From these the average width of the proximal rattle, corresponding to any length over-all  $L$  (but only in the adult range), may readily be computed by multiplication of  $L$  by the ratio set forth in the table.

Although the rattle statistics presented in the table represent the several species and subspecies with a moderate degree of accuracy, there need be no surprise if strings and proximal rattles are found to deviate appreciably from these figures in individual snakes. For there are not only dimensional fluctuations within homogeneous populations, but in all wide-ranging populations there are territorial differences as well. The table purports only to give species averages, which, at least, serve to indicate specific and subspecific characteristics and differences. In the future, additional specimens of some of the rarer forms will permit the correction of some inaccuracies caused by a lack of enough material to develop dependable averages.

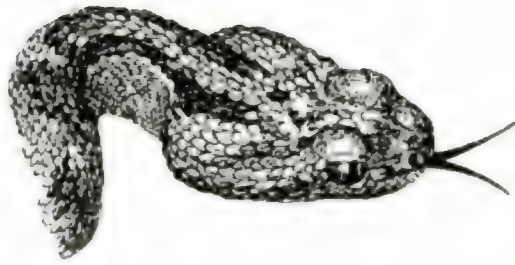
The rattles of the several species of rattlesnakes differ in form and color, as well as in size, but such differences are not sufficiently striking or constant to be always in evidence. It is, in fact, surprising to note the morphological similarity of the rattle, in species of rattlesnakes as widely different in other characteristics as some of them are. The general scheme of the interlock, the support effected by vertical asymmetry, the longitudinal side furrows, the tear-preventing bead or selvage, the fin-type reinforcements of the grooves—all of these intricate perfections are found in every species. The two incomplete lobes of the juvenile button are, in all forms, succeeded by the three fully interlocked lobes of the adult.

But there are differences in the angularity and radii of the curves of the lobes, as the rattles of some species have a more rounded appearance than others. This is particularly characteristic of *Sistrurus* and the smaller species of *Crotalus*, such as *pusillus*, *triseriatus*, *pricei*, *intermedius*, *willardi*, *lepidus*, *cerastes*, and *polystictus*. Of the larger species having this rounded form, *horridus* is the most outstanding. The *durissus* button is not only small, relative to the size of the snake, but has a somewhat unusual shape, in that the anterior lobe is relatively narrow (longitudinally) and the dorsal groove between lobes is especially deep, compared with other species.

Some of the smaller snakes, especially *polystictus*, *cerastes*, and *triseriatus*, have smaller transverse dimensions proportionate to the vertical than other species; also, some, particularly *cerastes* and *triseriatus*, are compressed longitudinally. Similar differences are sometimes evident between island forms and their mainland analogues.

When a rattle still surrounds the matrix, it is practically transparent and therefore seems to have the color of the skin below. However, when it has been cast off it loses its transparency (although remaining translucent) and through oxidation, or surface wear, assumes, in most species, a characteristic straw color. Some, however, take on a darker brown hue; this is particularly noticeable in *adamanteus*, *horridus*, *polystictus*, *lepidus*, *tigris*, *omiltemanus*, *willardi*, and all species of *Sistrurus*. *C. d. terrificus* rattles are often quite reddish.

The color of the rattle is entirely independent of the color of the matrix upon which it is formed; thus *ruber* rattles, formed on a black matrix, are light, whereas *tigris* rattles are dark, although the matrix is light gray or pink. The marks on the rattle matrices are a part of the body pattern of the snake, and are as consistent in color and pattern as the other marks on the tail.



## 6. Bodily Functions

### INTRODUCTION

Like all reptiles, rattlesnakes are under the dominant influence of external temperatures; they are the creatures of this phase of their environment. The most familiar of the larger animals about us—the mammals and birds—are, to a considerable degree, independent of the temperatures in which they live, particularly of short-range fluctuations, for they have internal heating and cooling mechanisms that maintain an almost constant internal temperature—a temperature that is an optimum for their metabolic processes and muscular activity. But the reptiles—ectothermic animals—are almost entirely lacking in this control; with falling exterior temperatures, their own bodily temperatures fall, with the result that the energy derived from oxidation declines, as do muscular activity and rate of digestion. At temperatures that would not be uncomfortable to a mammal or bird, a snake is reduced to enforced immobility. And, similarly, at above-optimum external temperatures, the lack of the cooling mechanisms of perspiration and a reduced effectiveness of evaporation from lung surfaces allow the body temperature also to rise, until at external temperatures that mammals withstand with no more than a moderate discomfort, the internal temperatures of reptiles rise to a dangerous degree; the muscle tissue hardens, circulation stops, and the animal dies. So important are these temperature effects on reptiles, so narrow the range of external temperatures in which their life activities may be carried on successfully, that their habits are largely circumscribed by their having to take the greatest advantage of favorable temperature conditions, and to avoid those that are detrimental or dangerous. When some objective—food, for example, or a protective refuge—can best be secured under unfavorable temperature conditions, a compromise results, with some sacrifice of the optimum condition for either category separately.

Another point to be borne in mind is the relative inactivity of snakes. Put briefly, it may be said that most of the time they do nothing; no enterprise or action is required of them. Their food and water needs are low compared with those of mammals and birds of similar size, for reasons discussed elsewhere (p. 665). Ordinarily they mate but once a year. With these two primal drives at a minimum, it follows that they have both long, and relatively frequent, periods of inactivity, extending, in summation, over a considerable part of their lives. In the interests of comfort, safety, and the preservation of energy, these times of rest are taken in suitable refuges, in holes, or under rocks or bushes. Thus they are secretive; they are not so often seen as other creatures having the same population density.

In the portrayal of the habits and reactions of rattlesnakes that follows, these themes of temperature effects and secretiveness will repeatedly occur.

In the discussion of rattlesnake habits and actions, some effort has been made to avoid anthropomorphisms, but without entire success. There is undoubtedly some variability in a rattlesnake's reaction to its surroundings and to unusual incidents—the approach of a human intruder, for example. To suggest that a rattlesnake's reaction to various stimuli is almost automatic and inflexible is certainly contrary to fact. Yet it is necessary to avoid the implication, so often given in accounts of rattlesnake activities, that we are dealing with a crafty creature of shrewd intelligence and cynical cunning—however more interesting this would make the narrative. On the contrary, the rattlesnake is an animal with fairly instinctive or stereotyped patterns of securing its primary needs of food, self-protection, and reproduction, but with some power of choice in meeting particular situations that may arise in the pursuits of these needs. But the intelligence with which the course is chosen is rudimentary and without predirectional calculation with respect to a goal to be attained.

#### GROWTH AND LONGEVITY

What we should like to know about rattlesnake growth is how fast and how steadily they grow; at what size and age they become sexually mature; whether growth continues beyond this age and to what extent; and how long they live. Of course, as rattlesnakes of the various species differ greatly in size, from some that are full-grown at a length of barely 2 feet and a weight of less than one-quarter pound, to others that may attain a length of 8 feet and a weight of 20 pounds or more, it is obvious that complete data on the growth curves of all the species and subspecies would be impracticably voluminous, if available at all, which they are not. Elsewhere (table 4:1) I have set forth certain bench-mark statistics of the several subspecies, including the average length at birth and the ultimate size attained by fully grown males. In the present section it is my purpose to discuss only rates of growth and development in example subspecies, selecting a few of the commoner kinds of rattlesnakes concerning which we have the fullest information. Even with respect to these, our data are not entirely dependable.

Information on rattlesnake growth and longevity may be gained from observations of captive specimens, or from marked specimens repeatedly recaptured in the wild. The former source yields information of somewhat doubtful validity because of the artificial conditions under which caged snakes live. The latter program, although achieving more accurate results, is so time-consuming that it has rarely been attempted; and, indeed, Fitch's studies (1949a, p. 531) indicate that capture and release may influence the subsequent activities of the snakes to such a degree as to affect normal growth trends to a serious extent. Even with captive snakes, it is so difficult to measure their lengths accurately without injury that reptile house operators are unwilling to submit their charges to such studies.

Snakes, rattlesnakes among them, do not attain a growth termination as sharply limited as in birds or mammals. In fact, it was once believed that they grew continuously until death, and that the largest individuals of a species were correspond-

ingly the oldest. Now it is known that they grow much faster as juveniles and adolescents than later; and, if growth does continue after the adult stage is reached, it is relatively slow. But, even so, the "knee" of the growth curve—the point of change from the adolescent to the adult rate—is less sharply defined than in the warm-blooded vertebrates, wherein the adult rate quite suddenly becomes zero. Petter-Rousseaux (1951, p. 191) experimented with the European ringed snake and concluded that growth, but at a much reduced rate late in life, continued practically throughout life. He determined age from growth ridges on the pterygoid bone. Brattstrom has found similar annual growth ridges in the skulls of rattlesnakes, and believes that they will be useful as age indicators. He finds the ridges easiest to determine on the frontal, although they are evident on many of the other bones.

One method of growth study is to compile the statistics of large numbers of individuals and correlate the lengths with the seasons. As long as the growth is rapid enough so that one can differentiate the several year-classes involved, this is a useful method of deducing average growth, each snake furnishing a single point on a scatter diagram. It has been used successfully with rattlesnakes during their first two years of life, when the number of rattles in the unbroken strings aids in segregating the classes. Beyond that age, it is practically impossible to segregate the age-classes, and therefore it is not feasible to determine growth trends of adults from this type of study. Such information must eventually come from periodic measurements of recaptured specimens in the field, a method that, in itself, may produce a disturbance of normal growth.

#### GROWTH VARIABLES AND DISPERSION

Even if narrowed to one single rattlesnake subspecies, we find the problem of determining the average rate of growth complicated by a variety of important differences—individual, sexual, and ecological. Examining the last factor first, we must remember that the division of a group of animals into subspecies—the most restricted class recognized nomenclatorially—does not by any means assure uniformity among the creatures so classified. This process of division is largely subjective, so that the degree of uniformity achieved depends on the ideas of the taxonomist who segregates and names the subspecies. Some taxonomists—the "splitters"—favor small, restricted subspecies differing from each other in only minor, but fairly consistent, characters; whereas their opposites—the "lumpers"—take a contrary view and recognize only forms that differ in much wider degrees and with greater concordance in the separating characters. But even the most confirmed splitter can never achieve complete uniformity in his ultimate groups, for animal variation is such that this degree of consistency is never attained. The differences in an animal's surroundings—the climate, topography, vegetation, food supply—all affect its growth; and since few subspecies inhabit a territory that is ecologically uniform, we find that an accurate growth curve for a creature in one part of its range may be inapplicable in another. For example, I have pointed out (1937, pp. 33–37) some of the differences that distinguish the prairie rattlesnakes (*C. v. viridis*) found in the vicinity of Platteville, Colorado, from those from near Pierre, South Dakota, about 375 miles away. These differences are by no means sufficient to warrant the assignment of separate subspecific names to the two popu-

lations, yet they do involve different growth curves, for the Pierre snakes are larger both at birth and maturity. Such intrasubspecific variations are everywhere apparent.

Sexual dimorphism in rattlesnake size was the subject of a study made some years ago (Klauber, 1937, pp. 12, 21), with the following conclusions respecting growth curves: At birth, male rattlesnakes average about 1 per cent longer than females. This increases to about 3 per cent in the following spring. In a composite population of adolescents and adults, the male superiority is 5 per cent. Sexual dimorphism becomes still further accentuated when the snakes are nearing the end of their second year. Among the fully matured adults it is probable that the males exceed the females in length by about 15 per cent, in most rattlesnake species. The only known exceptions are the sidewinders (*C. cerastes*), in which the adult females grow to be almost 10 per cent longer than the males (Klauber, 1937, pp. 24, 26; 1944, p. 98).

Finally, we have individual differences in the lengths of snakes of the same sex from the same area, and even from the same brood. This is the ordinary type of individual variation to which we are accustomed in the creatures all about us—in the pups in a litter or the chicks in a brood. We find that this range of variation tends to increase if we pool several litters or broods, even if the parents are all from the same area, and the broods were born at the same time. Lastly, there are differences in growth that become increasingly evident as the broods age, for some individuals remain stunted, while others grow amazingly. These differences are likely to be accentuated among wild creatures, some of which are more fortunate than others in securing food. Rattlesnakes, of any kind in any particular location, are subject to these same types of individual variability.

In an earlier paper (1937, pp. 7, 13, 19) I set forth the details of a study designed to determine the nature and extent of these individual variations among rattlesnakes, showing to what extent individuals deviate from the average of the group to which they belong.

First as to the variations within a brood: Calculations based on 31 broods comprising 320 young rattlers indicated a composite coefficient of variation of 4.5 per cent. Among these little snakes there were 4 so stunted that their survival would have been extremely doubtful; eliminating these reduced the coefficient of variation to 3.8 per cent. Eliminating a total of 11 freakish specimens—the 9 smallest and 2 largest—further cut the coefficient of variation to 3.3 per cent. A later study of the same kind, entailing 26 other broods totaling 241 young rattlesnakes, produced a composite coefficient of variation of 2.5 per cent, and this without any eliminations. I think we may safely conclude that brood coefficients of variation in length, unless such a brood contains one or more obvious defectives, will seldom exceed 4 per cent and will average 3.5 or lower. However, this statement is premised on the further assumption that the measurements are made soon after the young snakes are born, before postnatal differential growth has become important.

In the previous investigation, the shape of the dispersion curve was found to be approximately normal (1937, p. 11). Assuming a normal curve and a coefficient of 4 per cent, we may visualize the extent of the dispersion thus defined, by taking, as an example, a brood of red diamond rattlers (*C. r. ruber*) averaging 300 mm. (11.8 in.) in length. In such a brood, about half the little rattlers would vary be-

tween 292 and 308 mm. (11.5 and 12.1 in.) in length, and 90 per cent of the brood would comprise none shorter than 280 mm. (11 in.) or longer than 320 mm. (12.6 in.).

When we group young rattlers from different mothers, we find a definite increase in variation, as compared with the variation in a single brood. The increase results from a variety of factors, including inheritance,<sup>1</sup> differences between dates of birth and measurement, and within-brood variability in postnatal growth. Some of these factors produce different within-brood averages, thus increasing the group variation, even though the within-brood variation remains the same. For example, three large broods of prairie rattlesnakes (*C. v. viridis*), born within a period of four days to mothers from the same place in South Dakota, averaged 274.8, 304.0, and 319.2 mm. (10.8, 12.0, and 12.6 in.) respectively.

To determine the extent of the variation produced by grouped broods, studies were made of four groups, two of which were calculated in the prior study—the Zacatecas series of *C. m. nigrescens* and the San Patricio series of *C. atrox* (1937, p. 10, table 7)—whereas the other two were computed from more recently acquired series of prairie rattlesnakes from Bonesteel and Timber Lake, South Dakota. None of the little snakes had been fed. The coefficients of variation were found to be as follows:

Series	Specimens	Coefficient of variation
Zacatecas . . . . .	82	5.26
San Patricio . . . . .	139	5.12
Bonesteel . . . . .	79	5.15
Timber Lake . . . . .	96	6.51

The expected increase above the within-brood variation is apparent. The higher variation of the Timber Lake series, as compared with the others, was probably related to a longer interval between birth and measurement. I conclude that groups formed of several broods, mixed together and measured soon after birth, usually have coefficients somewhat below 5.5 per cent.

The next stage investigated consisted of two lots of young-of-the-year captured at the dens at hibernating time. Both lots—one of 152 snakes, the other of 229—were prairie rattlers (*C. v. viridis*). Their coefficients of variation in length were 7.9 and 8.7 per cent, respectively. This increase from the 5.5 per cent of the pooled broods may be attributed largely to the good fortune—or the lack of it—experienced by the little rattlers in the interval of about two months between birth and hibernation. The marked effect of food on the growth of young rattlers is quite apparent from observations of captive young; those that secure food soon outdistance their brothers that have had none. Another condition tending to increase the dispersion in size in the young-of-the-year at the dens is the fact that there may be a difference of as much as two or three weeks between the dates of their births. There is still another factor, however, that should have a contrary effect, namely, the elimination of the stunted and defective young. These little creatures, some blind, some with distorted bodies, are commonplace among captive-born broods, and certainly, if present in wild broods, their survival must be brief.

<sup>1</sup> R. M. Perkins (by letter) has suggested that, in any subspecies, the young snakes in the smaller broods average longer than those in the larger broods. I have not found this to be the case, although it is true that smaller mothers have fewer young than do the larger.

Subsequent to their leaving the dens in their first spring, it is difficult to segregate any age-class in order to determine the nature of the dispersion. Sexual dimorphism in length becomes increasingly important; starting with a male superiority in the broods of only 1 per cent, it becomes 2 per cent or more at the dens and probably reaches 4 or 5 per cent by the following summer. From this time on, the males continue to outgrow the females until a male superiority in length of about 10 to 15 per cent is ultimately attained in the adult snakes. Rattle studies indicate that the divergence is accentuated after the age at which the snakes attain their seventh rattle, which is about two years in the rattlers of southern California, and somewhat more in the areas where the snakes have shorter growing seasons.

To return to the variation among rattlers of the same age-class, I should estimate that, if the sexes be considered separately, rattlers at the age of 8 months to a year would have a coefficient of variation in length of 10 to 12 per cent, probably increasing to 15 per cent when the snakes are fully mature. This presupposes snakes from a single area, not subject to different ecological effects. Admittedly these are hypothetical figures, for we know of no way in which the several age-classes of rattlesnakes over two years old may be segregated, many of the larger, faster-growing individuals having long since overhauled and passed some of the slower-growing snakes a year or more older. Even the segregation of the snakes spending their second winters at the dens—at an age of about 16 months—from their fellows one or two years older, is not possible with entire accuracy, although those having unbroken rattle strings can be allocated with some assurance.

If we assume a 15 per cent superiority of adult males in length and a 15 per cent coefficient of variation within each sex, it may be of some interest to cast these figures into the more practical statistics of a particular snake population. Assume that fully adult male red diamond rattlers (*C. r. ruber*) in northern Baja California<sup>2</sup> average 4½ feet (54 inches long). Then the average female measures 3 feet 11 inches. Half the males will range between 4 feet ½ inch and 4 feet 11½ inches, and half the females from 3 feet 6 inches to 4 feet 4 inches. Ninety per cent of the males should fall between a minimum of 3 feet 4½ inches, and a maximum of 5 feet 7½ inches; and the same proportion of females will range between 2 feet 11½ inches, and 4 feet 10½ inches. It is interesting to note that under this theory of deviations from the average, about one rattler out of every 100 adult males of this subspecies should be 6 feet or more in length; however, there is evidence that the extremes do not follow the normal curve and I claim no accuracy for this calculation.

#### GROWTH CURVES

Having presented data in terms of the coefficient of variation, to indicate the extent to which individual snakes deviate from the average of their broods, groups, or age-classes, I shall turn now to the growth curve of the hypothetical average rattlesnake. But although the dispersions that I have given in terms of coefficients, or percentages, of length are probably equally applicable to all subspecies of rattlers—provided they are territorially homogeneous—it is obvious that a growth curve, that is, a statement of the length of an average rattler at different ages, must be different for every subspecies. Indeed, there will not be consistency within a sub-

<sup>2</sup> I select this as being a comparatively primitive area where the larger snakes have not been killed off as consistently as in San Diego County, California.

species, unless it occupies a particularly uniform territory. Under these circumstances we cannot survey the entire field, but must restrict our studies to homogeneous groups. Two of these have been available to me in adequate numbers to permit some conclusions respecting growth rates—series of the southern Pacific rattler (*C. v. helleri*) and of the red diamond (*C. r. ruber*) from San Diego County, California.

From these series, scatter diagrams were made by means of entering each specimen as a single point on the diagram, the abscissa representing the date of preservation, and the ordinate the length of the snake in millimeters.<sup>3</sup> If the rattle string was complete, the point was designated by the number of rattles in the string; if not, by a cross. The sexes were distinguished by colors. In these scatter diagrams certain concentrations of the points into zones were at once evident, particularly for the first two years of the life of the snakes. From these, average trends could be deduced, with considerable accuracy up to the second hibernating season, and more doubtfully thereafter.

*Growth of the Southern Pacific Rattlesnake (C. v. helleri).*—This description of the growth curve (fig. 6.1) of the southern Pacific rattlesnake (*C. v. helleri*) is based on 829 specimens from San Diego County, California.

Although a few young appear as early as the first of September, most of the births in this territory occur after September 15, and the young-of-the-year begin to be seen on the roads after the 20th. While the size at birth probably averages between 275 and 280 mm. (10¾ to 11 in.), most of the young found in the wild in late September and October run from 300 to 340 mm. (11¾ to 13½ in.). It is probable that there is some growth resulting from the absorption of the egg yolk, as young rattlers are puffed up with this food supply when born. Also, there is an early elimination of defective young, and this tends to increase the average length, for many of the defectives are stunted.<sup>4</sup> The little snakes enter their first hibernation at a length of about 350 mm. (13¾ in.). Most of them have only a button, although a few—somewhat less than 20 per cent—have attained their second rattle segments.

While the young rattlers in this area are to be found occasionally roaming about in December, January, and February, they are definitely less plentiful after November 15, and commonly do not emerge from hibernation until about March 10. At this time they continue to average about 350 mm. (13¾ in.) and all but a few still have only a button.

By mid-April an increased divergence in size becomes apparent, evidently as a result of success or failure in obtaining food. The average size is then about 380 mm. (15 in.), most of the individuals falling between 310 and 460 mm. (12¼ and

<sup>3</sup>These studies were made on the measurements of specimens immediately after being killed, while still limp so that they could be laid along a ruler, and thus measured accurately. Specimens already stiffened in preservative cannot be measured so accurately; and even when they can be straightened, will have been subjected to some shrinkage, which studies have shown to be about 2 per cent. Skins cannot be used in length studies as they involve stretching by as much as 35 per cent, thus entailing great inaccuracy. Data of value can be had from live specimens, but with some hazard both to the snakes and to the investigators. It will usually require two persons to control a snake, for it must be stretched and held for several moments until the muscles become tired and relaxation ensues. With some experience, live specimens can be measured with an individual accuracy of about 3 per cent, and a cumulative accuracy within 1 per cent, as verified by sample groups measured first alive and then dead.

<sup>4</sup>There is evidence of the elimination of deviators from the normal, even though their abnormalities are apparently not of a detrimental character.

18 in.). A few have 3 rattles, but the majority are divided evenly between those having 1 and 2. (Young rattlers having only a button are found in every month of the year. They comprise the smallest proportion of the population in July and August, just before the new crop appears; but they are present in considerable numbers even as late as June. Whether these remaining single-rattle young were born, as were most of their class, in the previous September, or whether some are the result of off-season births in the spring, I do not know. A few, at least, are from mountain areas, where the shorter active season has a retarding effect on growth.)

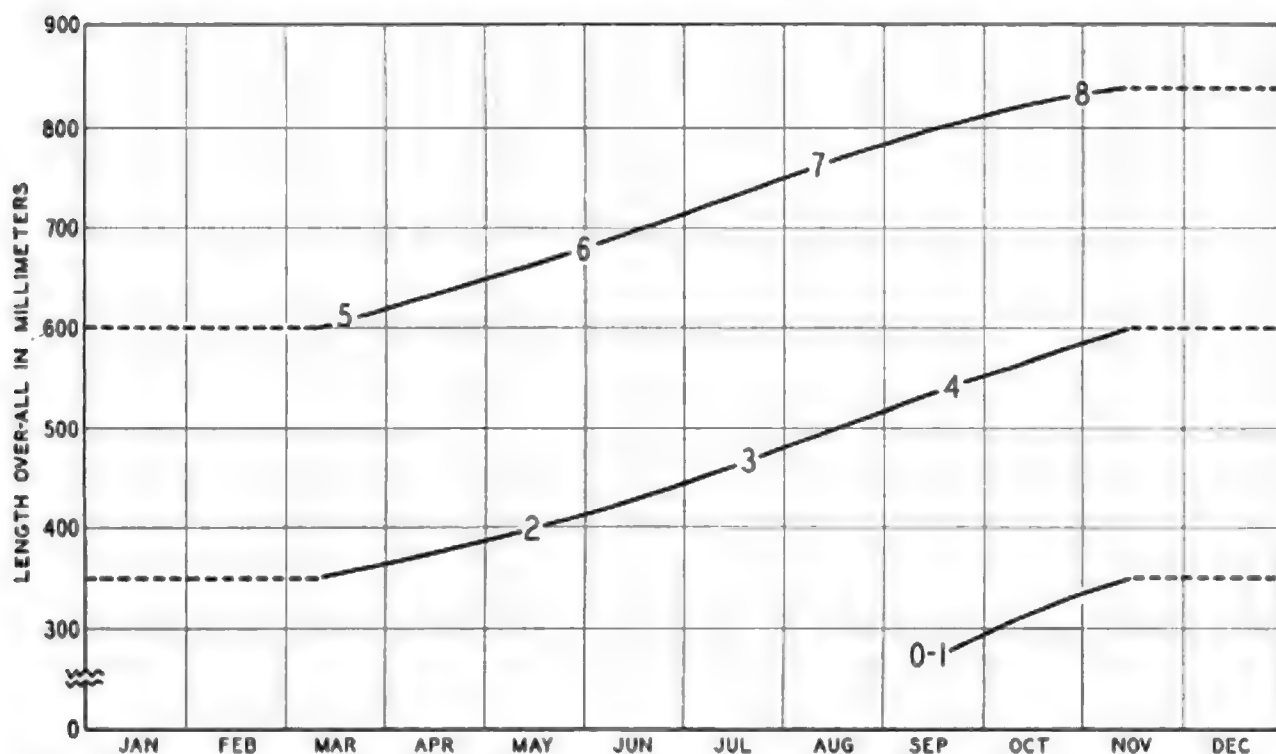


Fig. 6:1. Growth of the southern Pacific rattlesnake (*Crotalus viridis helleri*) during its first two years. The curve for the last half year is applicable only to males. (The numbers indicate the number of segments in unbroken rattle strings.)

In May the average length of the young-of-the-year is about 400 mm. (15¾ in.) with a range of 310 to 500 mm. (12¼ to 19¾ in.). Two-rattle strings predominate, but there are many ones and threes, with an occasional four.

By June the mean length has increased to 430 mm. (17 in.) and a few have grown to 580 mm. (22¾ in.), although others are as short as 310 to 320 mm. (12¼ to 12½ in.). Two-rattle strings remain slightly in the majority, although there are many threes and fours.

In July the average length exceeds 450 mm. (17¾ in.); in fact, toward the end of the month it approaches 500 mm. (19¾ in.) and 3 rattles have become the mode.

By August the mean is a full 500 mm. (19¾ in.), and in September, when the snakes are one year old, the average length is about 540 mm. (21¼ in.) and 4 rattles are the mode. Thus the average increase in length during the first year is about 94 per cent. The snakes go into hibernation at a length of about 600 mm. (23½ in.) and usually with 4 or 5 rattles, the latter number probably predominating.

In the succeeding year they emerge at the same length and grow to 700 mm. (27½ in.), or slightly more, by June. On their second anniversaries, in September,

the males somewhat exceed 800 mm. ( $31\frac{1}{2}$  in.), but the females do not average much above 720 mm. ( $28\frac{1}{2}$  in.). They probably enter their third hibernation but little above these lengths, and would have 8 or 9 rattles, were the strings complete, which is not usually the case.

Comparing the schedule above outlined with that previously published (Klauber, 1937, p. 16, fig. 3), I find that the additional specimens accumulated during the past 10 years have caused me to raise slightly (about 20 mm. or  $\frac{3}{4}$  in.) the length attained as of each month, but to retard, by about a month or so, the acquisition of each rattle. Admittedly the data for the second full growing season are too meager to afford confidence in the results; I consider this curve to be less assured than that of the subspecies that follows, as far as the trend in the second growing season is concerned. As to the third full season, I have data leading me to believe that the males would average about 900 mm. ( $35\frac{1}{2}$  in.) in June, and would have 9 or 10 rattles, were the strings unbroken. But this is to be taken only as a preliminary estimate.

*Growth of the Red Diamond Rattlesnake (C. r. ruber).*—The following summary describes the growth of the red diamond rattler based on a scatter diagram of 249 specimens from San Diego County, California. Data are presented for the first  $2\frac{1}{2}$  years of the snakes' lives, although the separation of the age-classes is not distinct enough to permit drawing conclusions with complete assurance beyond one year. The results are shown in figure 6:2.

The young snakes begin to appear in early September, although most broods are probably born in the latter half of the month. They average about 300 mm. ( $11\frac{3}{4}$  in.) at birth. The prebutton, or birth rattle, is shed about 7 to 10 days after birth.

By mid-October many, if not most, of the little rattlers have obtained food. Some of the weaklings have no doubt been eliminated; and, partly through growth, and in part resulting from the failure of the smallest to survive, the average length has become 350 mm. ( $13\frac{3}{4}$  in.). There is a further growth to about 390 mm. ( $15\frac{1}{4}$  in.) in November. A few individuals have acquired their second rattle segments by November 10, but it is probable that the majority enter their first hibernation with only a button.

From December to February, inclusive, too few specimens are captured to determine any growth trends; it is probable that almost no growth takes place during these months when the snakes remain in seclusion except on especially warm days.

In March—about the middle of the month, in years of average temperatures and rainfall—the little rattlers begin to appear, but they do not become really plentiful until mid-April. By this time an average length of nearly 500 mm. ( $19\frac{3}{4}$  in.) has been reached. It is apparent that many of the snakes shed upon issuance from hibernation, for 2-rattle strings are in the majority in March and early April, although stragglers with only a single rattle are still evident until mid-May.

By mid-April the average length has exceeded 500 mm. ( $19\frac{3}{4}$  in.) and at this time the snakes enter a period of rapid growth. Toward the end of April, 3 rattles become the mode. Some specimens attain a length of 600 mm. ( $23\frac{1}{2}$  in.) at this time, and few have failed to reach at least 450 mm. ( $17\frac{3}{4}$  in.). The smaller individuals still have only 2 rattles.

In May the mean length has increased to about 550 mm. (21¾ in.), most individuals falling between 450 and 650 mm. (17¾ and 25½ in.).

The first snakes with 4 rattles appear in June, although 3-rattle strings remain the mode during this month, and snakes with only 2 are still present in considerable numbers. The average length is close to 560 mm. (22 in.) and the range 460 to 670 mm. (18 to 26½ in.).

In July, with omission of a few exceptional specimens, the range in sizes is from 500 to 700 mm. (19¾ to 27½ in.), the average being about 610 mm. (24 in.).<sup>5</sup> The

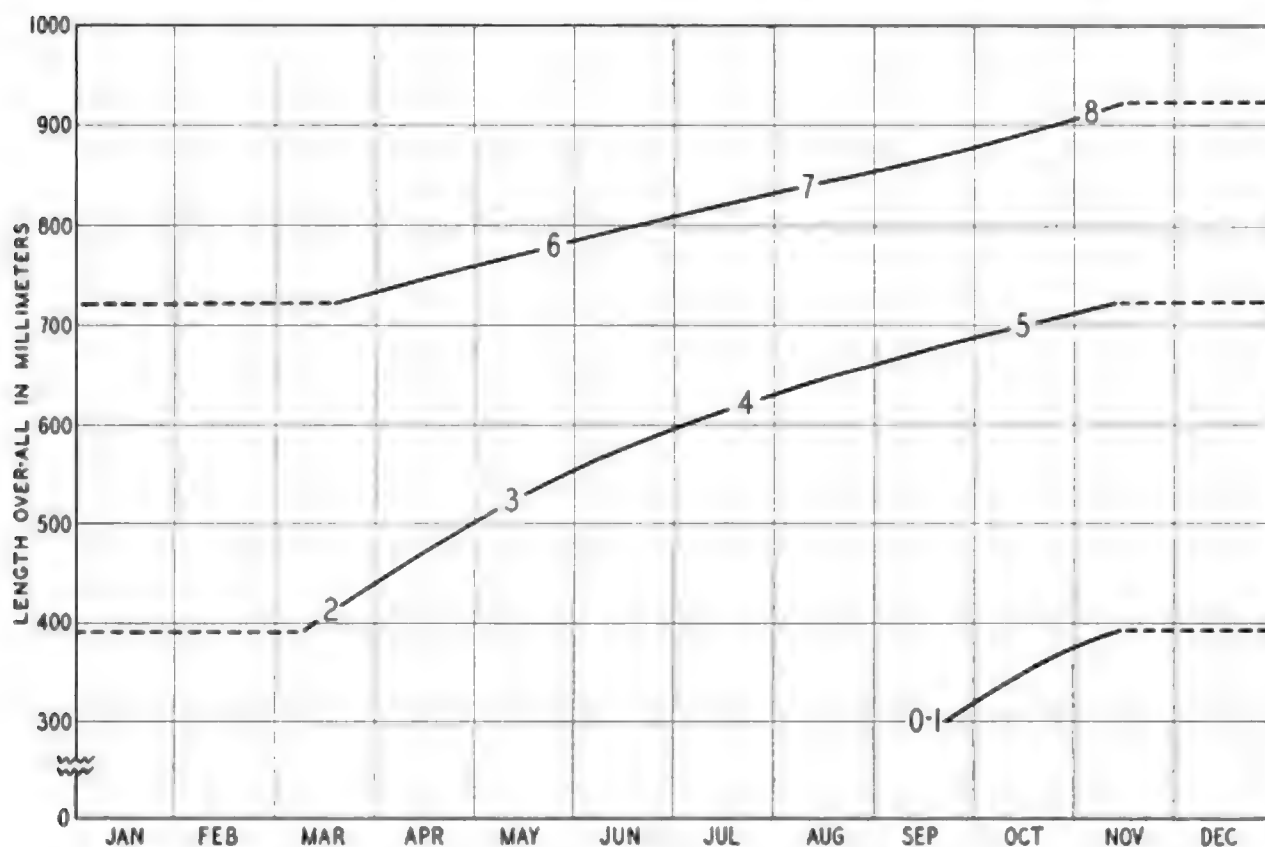


Fig. 6:2. Growth of the red diamond rattlesnake (*Crotalus ruber ruber*) during its first two years. The curve for last half year is applicable only to males. (The numbers indicate the number of segments in unbroken rattle strings.)

first snakes undoubtedly of this age-class with 5 rattles have appeared, and strings with 4 are in the majority.

The August average is about 640 mm. (25¼ in.), and in September the young snakes have reached 670 mm. (26½ in.). Thus, by the time they are one year old, they have somewhat more than doubled their lengths. During the preceding active months they have grown at a rate of about 30 mm. (1.2 in.) per month.

From this point, the growth trends can be traced only with much less assurance. It is believed that the snakes go into their second winter seclusion at an average length of about 720 mm. (28½ in.), with a variation of most specimens between 610 and 830 mm. (24 to 32¾ in.), and that 5 rattles are the mode.

In the following spring the average length increases to 750 mm. (29½ in.) and 6 rattles become the prevailing number by June, at the latest. From this time on, incomplete strings become more prevalent. I judge that these young rattlers reach

<sup>5</sup> As a partial confirmation of this figure it may be noted that the slightly smaller San Lucan diamond rattler (*C. r. lucasensis*) at this age average 550 mm. (21¾ in.).

their second birthdays with an average length of about 870 mm. (34¼ in.) and with 7 or 8 rattles. Sexual dimorphism has become accentuated, the males exceeding the females in length by at least 10 per cent. It is my opinion that they retreat into their third hibernation with the males averaging about 940 mm. (37 in.) and the females 850 mm. (33½ in.). By early next spring they have gained about 25 mm. (1 in.) and 9 rattles have become the mode, although some individuals may have as many as 11 and others as few as 5. Less than half the specimens at this age have complete strings.

From this point on it is impossible to trace the growth, for the scattering makes the segregation of the age-classes impossible. The final length attained is hard to judge; males 1,300 mm. (51 in.) long are not exceptional in primitive areas.

In interpreting these data on the growth of rattlesnakes during their first two years of life, no one should expect every *helleri* or *ruber* found in San Diego County to fall close to these age-length trend lines. I have already called attention to the extent of the deviations from these averages. Not only will discrepancies in length at specific dates be found, but variations in the number of rattles as well—discrepancies both in the length at which a snake attains a particular rattle (in terms of its serial number in a complete string), and also the month of the year in which that rattle is attained. For there are dispersions in these rattle relationships as well as in the correlation of length with age (see p. 314).

*Validity of Growth Trends.*—The question may well be asked as to the general accuracy of these growth statistics—particularly whether there is any possibility of my having crowded three years of actual growth into what I have interpreted as being only two years. A. M. Jackley, for example, believed that rattlers emerge from their second hibernation (at an age of about 21 months) with 4 rattles and enter their third hibernation (age about 27 months) with only 5. But I find with respect to both the large series of prairie rattlers (*C. v. viridis*) collected at hibernating time at Platteville, Colorado, and at Pierre, South Dakota, that the heavy concentration of individuals—among those having unbroken strings—with 5 rattles proves, without question, that they are representative of the next age-class beyond those with 1 and 2, which, from their size, can only be young-of-the-year. Should I have exaggerated the rate of growth during the first full year of activity, an intermediate class would be present, represented by snakes having 3 rattles at the time of their second hibernation. Yet snakes with 3 rattles at this time of year are virtually nonexistent. Similarly, snakes of an appropriate length to fill the requirement of an intermediate age-class are absent. For example, in the Platteville series such an intermediate class—between the obvious young-of-the-year and those centering in the 5-rattle class—would have a length at hibernation time of about 420 mm. (16½ in.). Yet, in this series, out of 858 rattlers taken at the hibernating dens, only 8 snakes fall in the range of 370 to 480 mm. (14½ to 19 in.); and there were only 19 specimens between 350 and 510 mm. (13¾ and 20 in.). This gap can be interpreted only as one between age-classes; and there is no alternative to the conclusion that these Platteville prairie rattlers enter their second hibernation with a mode of 5-rattle strings, just as do the snakes of San Diego County. Figure 6:3 shows the population distribution to which reference has been made, with the gap clearly evident.

These statistics have been used merely to indicate that I have not completely overlooked an intermediate age-class; they should not be taken as proof that the South Dakota or Colorado snakes grow as fast—in terms of the percentage of full adult size—as the rattlers of San Diego. On the contrary, the shorter growing season cannot but have some effect; and there are indications that the South Dakota snakes, although they shed as frequently as the San Diego snakes, at least up to their

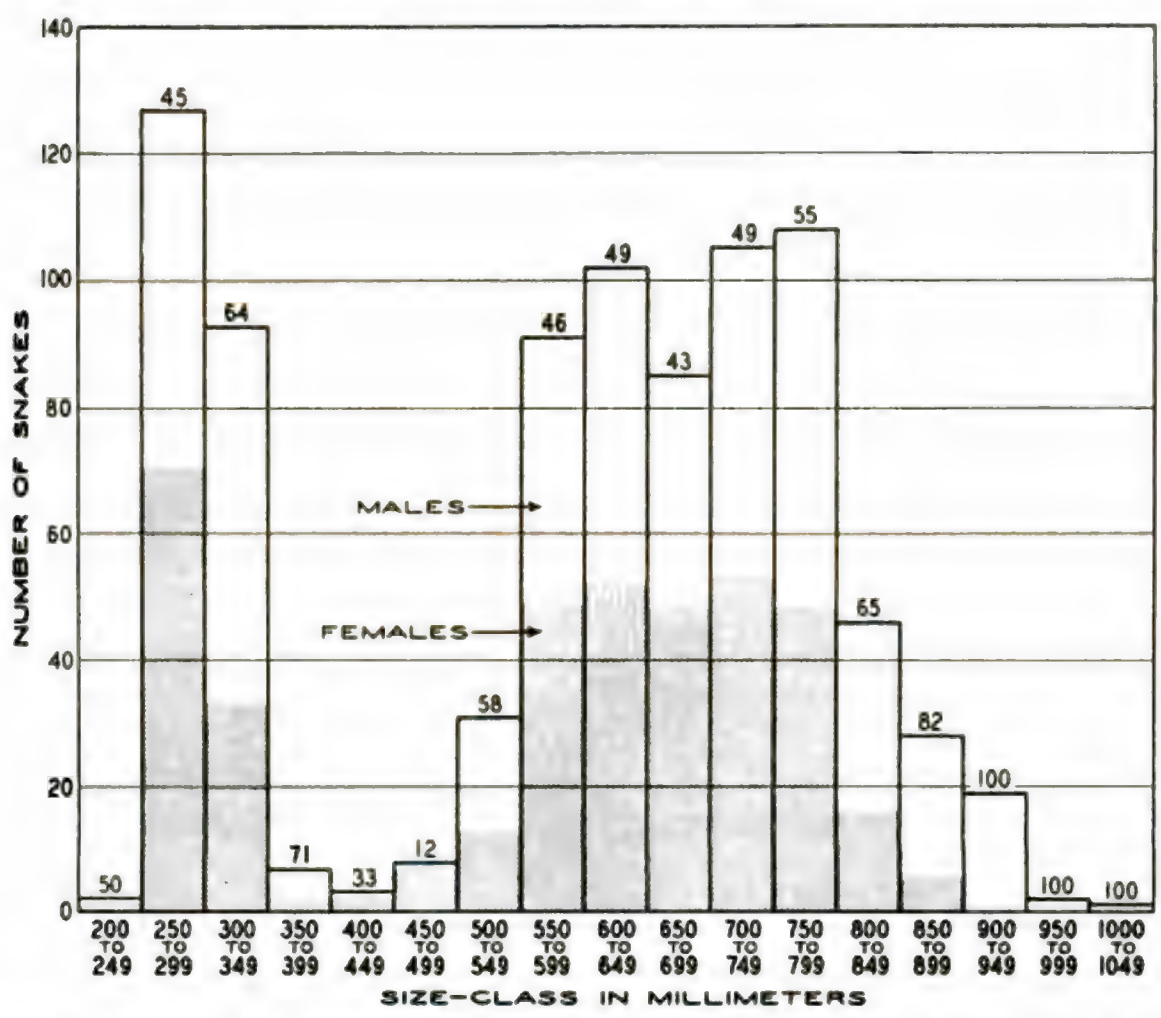


Fig. 6:3. Distribution of a snake-den population by size and sex, as found in a series of prairie rattlesnakes (*C. v. viridis*) from Platteville, Colorado. The series included 459 males and 399 females, total 858 snakes. (The figures at the tops of the columns indicate the percentage of males in each size class.)

second hibernation, may gain a smaller proportion of their ultimate lengths during their first two years of life than the San Diegans, and may average 2, rather than 3, sheddings during their second active season.

Aside from the statistics discussed above, the most complete studies on the growth of the rattlesnake thus far made available, have been those of Fitch and Glading (1947, p. 103) and Fitch (1949a, p. 519). These were made on the northern Pacific rattler (*C. v. oreganus*) on the San Joaquin Experimental Range in Madera County, California. They involved an extensive and painstaking program of measurement, release, and recapture. Although the data are not exactly comparable with the *helleri* averages that I have set forth, the general conclusion indicates a somewhat slower relative growth and frequency of rattle acquisitions than the difference in the lengths of the growing seasons in Madera and San Diego counties might lead

one to expect. However, it is to be noted that most of the specimens captured, before being released, were palpated to ascertain the stomach contents. With so nervous a creature as a rattlesnake, this probably had some effect, at least for a time, on feeding and growth, as admitted by Fitch and Glading (1947, p. 118) and Fitch (1949a, p. 531). It is remarkable that two of the young snakes they captured (p. 115 and p. 534) showed neither growth nor shedding during an interval of about a year. Another shed twice but failed to gain in either length or weight in a year. The authors attribute instances of this kind to a failure to obtain food, and presume that such individuals are destined to early elimination. It is obvious that, with my method of determining growth curves by averages, such individuals as these would be improperly allocated; and, if they are present in any great numbers in a rattlesnake population, would seriously distort my results.

Another study of growth in the rattlesnake is that of Heyrend and Call (1951, p. 28) made on the Great Basin rattler (*C. v. lutosus*) in the vicinity of Salt Lake City, Utah. As might be expected in an area with a more severe climate and shorter growing season than southern California, smaller annual increments in length were evident than in the subspecies *C. v. helleri* in San Diego County.

Such data on growth as we have been able to secure from captive specimens at the San Diego Zoo tend to confirm the size-time statistics that I have given for San Diego County *helleri* and *ruber*; at least there is no indication that the rate of growth has been exaggerated by our entirely overlooking an age-class.

It is believed that rattlers are sexually mature and mate for the first time after issuing from their third hibernation, at an age of about  $2\frac{1}{2}$  years. In the southern areas, where annual broods are the rule, the females would then have their first young at the age of three years; but in the north, where they cannot be brought to term in a single growing season, the earliest young would not be born until their mother's fourth birthday, and probably, in some cases, not until the fifth.<sup>6</sup> At the San Diego Zoo, two females that had mated in the wild gave birth to young when their rattles comprised unbroken strings of 9. This would tend to verify their having their first broods on their own third anniversaries.

The extent to which the growth trends evident in the San Diego County *helleri* and *ruber* apply to other subspecies of rattlesnakes can only be surmised. No doubt most southern species approximately double their lengths during their first year of life.<sup>7</sup> In each rattlesnake subspecies, the largest males eventually attain a length of from  $3\frac{1}{4}$  to 5 times their lengths at birth. The lower figure applies to the smallest species and the higher to the largest; put in other words, it may be stated that the smaller species of rattlesnakes are proportionately larger at birth than the larger species, as set forth in another chapter (p. 174). The same is true of subspecies; stunted races are proportionately not as small at birth, compared to their full-sized relatives, as at maturity. Stunting is, in part therefore, effected in the postnatal stage and is not the result of a uniform reduction from fertilized egg to maturity.

Some idea of the factors related to subspecific differences in growth and ultimate

<sup>6</sup> Volsøe (1944, p. 35) found that the males of the European viper (*Vipera berus*) in Denmark produce sperm at an age of  $4\frac{1}{2}$  years and the females first have young at 5 years.

<sup>7</sup> Imler (1945, p. 267) found that the bull snakes (*Pituophis catenifer sayi*) of Nebraska approximately doubled in length during their first year. Data on growth in other genera will be found in Blanchard and Finster (1933, p. 344) and Volsøe (1944, p. 34).

size may be gained from noting the ecological differences obtaining in some of the areas in which related forms of different sizes occur. It is apparent that the food supply and the length of the growing season are the most important influences. The largest rattlers occur in areas where suitable food is plentiful, both for the young and adults, and where the growing season is relatively long, for the outstanding species are the eastern diamondback (*C. adamanteus*), the western diamond (*C. atrox*), the canebrake (*C. h. atricaudatus*), the Central American rattler (*C. d. durissus*), and the Mexican west-coast rattler (*C. b. basiliscus*). All of these occur in favorable situations in our southern states or Mexico. Similarly, the largest subspecies of polytypic, wide-ranging species are found in the most favorable areas. For example, the canebrake rattler is larger than its less favorably situated relative, the timber rattler (*C. h. horridus*); and the western diamond (*C. atrox*) grows to a larger size in Texas than in more arid areas farther west. Most mountain species of rattlesnakes—*C. pricei*, *C. triseriatus*, *C. intermedius*, and *C. willardi*, for example—are notably small; and species that range from lowlands into the mountains are generally of reduced size at the higher elevations. This is true of the various subspecies of the western rattlesnake (*C. viridis*).

The Mojave Desert sidewinder (*C. c. cerastes*) is smaller than its Colorado Desert relative (*C. c. laterorepens*); this may be correlated with a shorter growing season. But the smallness of the Arizona prairie rattler (*C. v. nuntius*), compared to the prairie rattlers (*C. v. viridis*) from farther east and north may be the effect of a reduced food supply rather than a climatic difference. In suggesting the correlations of these factors with size, I am not, of course, implying a direct Lamarckian result; rather, I wish to indicate that small size may be the result of natural-selection trends where food supply and temperature-mass relationships give the smaller individuals a competitive advantage.

Although these differences in ecology may explain some of the variations in rattlesnake size, particularly within a single species, they are far from explaining all the differences that exist among rattlesnake species. For example, the largest of all rattlesnakes, the eastern diamondback (*C. adamanteus*), has a range almost coincident with one of the smallest, the pigmy rattler (*S. miliarius*). Thus similar ecological conditions have produced, or at least have proved quite satisfactory for, entirely different creatures, speaking in terms of size.

Island subspecies are usually small; this may sometimes be explained in part by unfavorable climate or food supply, but not always. Probably the Coronado Island rattler (*C. v. caliginis*) is stunted, compared to its mainland relative, the southern Pacific rattler (*C. v. helleri*), because the climate of the island on which it lives is unfavorable, fog-enshrouded as it is for weeks at a time; and the same reasoning may explain the relationship between the Cedros Island rattler (*C. exsul*) and the mainland red diamond (*C. r. ruber*) from which it was originally derived. But these simple and logical reasons fail to explain why the red diamond rattlers (*C. r. ruber*) of Ángel de la Guarda Island are smaller than their mainland relatives, whereas the speckled rattlers (*C. m. pyrrhus*) on the same island are larger than those on the mainland.

Similar differences are evident in other genera of snakes. Volsøe (1944, p. 38) has

\* Allen and Neill (1950c, p. 35) believe this subspecies to attain a length of 5 feet at the age of 3 years.

discussed corresponding variations among the European vipers (*Vipera berus*). Stradling (1881, p. 148) claimed that snakes from England grew to larger than natural size when removed to the tropics, but it may well have been that the changes observed resulted from the other modified conditions incident to captivity.

#### WEIGHT

In the paper devoted to studies of growth, to which reference has repeatedly been made (Klauber, 1937), although most of the data considered growth in terms of length over-all, certain correlations between length and weight were also established (p. 41). The purpose of the study was to develop the mathematical nature of the relationship, that is, the character of the average length-weight regression curve; the extent of the deviations of individual specimens from that curve; and, finally, the extent of sexual dimorphism.

It was found possible to attain consistent solutions of these problems when adequate series of specimens representing homogeneous groups were available. Live, or freshly killed, snakes were found necessary, as preserved material produced completely undependable results because of the effect of preservation on weight. Series representing all ages yielded the most trustworthy trend lines. Snakes fresh from the wild were used wherever possible, to avoid the uncertain effects of captivity on the feeding schedules and therefore on normal weight.

The regression curve of weight on length for rattlesnakes was found to adhere to the form  $W = CL^P$ , where  $W$  is the weight,  $L$  the length over-all, and  $C$  and  $P$  are constants, although having different values for each of the several species investigated. This form of curve is to be expected in regression lines of weight on length. It is, fortunately, an easy form to investigate graphically since it reduces to a straight line on log-log co-ordinates.

Combining the sexes, I have found that the two forms for which the most extensive series were available—the western diamond rattler, *C. atrox*, and the related diamondbacks, such as *C. r. ruber*; and the western rattler, *C. viridis*, and its subspecies—adhered rather closely to the equation  $W = 550L^{3.3}$ , where  $W$  is expressed in grams and  $L$  in meters.

The fact that the exponent in the equation exceeds 3 indicates that these rattlesnakes do not retain a constant body shape, assuming no change in specific gravity, but become somewhat heavier-bodied or stouter with age.

In order that the relationship between length and weight, as specified by this equation, may be more clearly understood, table 6:1 is presented, showing the weights at various arbitrarily selected lengths.

The outstanding feature of these tables is the rapid increase in weight, for proportionately small increases in length, as the larger sizes are approached. A 6-foot rattlesnake is seen to be almost twice as large, in terms of weight, as a 5-footer.

In addition to the tables, the relationship implied in the equation  $W = 550L^{3.3}$  is also set forth in figure 6:4, from which the weight at any length can be readily determined.

The generalized curves applicable to *C. atrox*, *C. viridis*, and their close relatives were found not to represent some species of rattlers, which differed significantly from these in body proportions. The most conspicuous variant was *C. cerastes*,

which was found to follow the regression line  $W = 930L^{3.42}$ , indicating a thicker, heavier-bodied snake than the others. No doubt studies of other species would develop similar differences.

These equations correlating rattlesnake weights with lengths are of interest as indicating averages, but, of course, it is to be expected that there is a considerable variability in individuals—that is to say, not all rattlesnakes of a given species at a specific length (4-foot red diamonds, for example) weigh the same. My studies indicated a virtually constant percentage of deviation from the regression line throughout life and that cross sections of the dispersion surface are normal curves, with a standard error of estimate at any length of about 18 per cent. From this it

TABLE 6:1  
APPROXIMATE RELATIONSHIP BETWEEN LENGTH AND WEIGHT IN RATTLESNAKES

Metric measure		English measure		
Length, mm.	Weight, grams	Length, feet	Weight	
			Pounds	Ounces
250	5.7	1	.	0 4
300	10.4	1½	..	1 5
350	17.2	2	..	3 8
400	26.8	2½	..	7 9
500	57.2	3	..	14 5
700	170	4	2	5 0
1,000	550	5	4	14
1,500	2,096	6	8	14
2,000	5,417	7	14	13
2,500	11,310	8	23	0

may be deduced that half the rattlesnakes of a given length will be no more than 12 per cent heavier or 12 per cent lighter than the average weight for that length, as determined from the curve; and that 90 per cent will differ from the average by no more than 23 per cent. The correlations between length and weight were set forth in another study, in terms of the coefficient of correlation (Klauber, 1945, p. 62).

Sexual dimorphism in weight was also investigated. It was found that both constants, the coefficient of  $C$  and the exponent  $P$  in the equation  $W = CL^P$ , were higher for the females than the males. This means that the adult females are heavier than the males of similar length; the difference in favor of the females was found to be about 20 per cent at their full growth. However, it must be remembered that adult males in most species reach lengths up to 15 per cent greater than the longest females. This greater length more than compensates for the somewhat stouter habitus of the females, so that the heaviest rattlesnakes are males.

Studies were made of the Pierre and Platteville series of prairie rattlesnakes (*C. v. viridis*) before the beginning and after the end of hibernation, and the conclusion was drawn that the adults lose about 4 per cent in weight during hibernation, and juveniles about 20 per cent. There is virtually no increase in length during this period of seclusion.

A scatter diagram showing the length–weight relationships of female northern Pacific rattlesnakes (*C. c. oreganus*) will be found in Fitch and Glading, 1947, p. 118. Their snakes are found, on the average, to be somewhat heavier for a given length than the prairie rattlers (*C. v. viridis*) from which my curves were deduced. Fitch (1949a, p. 522) has discussed the variations in the weights of individual snakes after successive releases and recaptures. He found their weights to fluctuate in an irregular and unpredictable manner. Handling seemed to have an adverse effect,

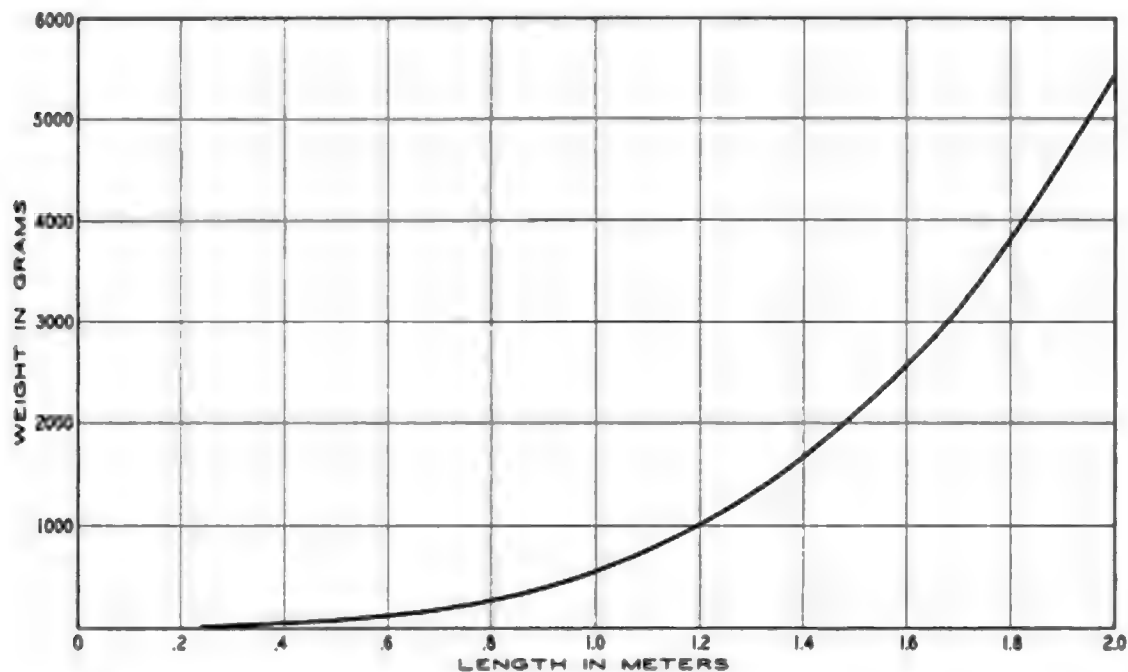


Fig. 6:4. Approximate relationship between the over-all length and the weight of western diamond rattlesnakes (*C. atrox*) and western rattlesnakes (*C. viridis*).

especially on the young. A young female captured six times within a two-month period lost almost half its weight.

LONGEVITY

Such data as we have on the age that rattlesnakes attain must come from observations of captive snakes, for no program of field observations by capture and release has reached such a duration as to encompass the probable normal life of rattlesnakes.

Some of the records cited in the literature are as follows: Say (1819, p. 263) mentions a timber rattler (*C. h. horridus*) that had been in captivity 10 years at the time of its death. Holbrook (1842, vol. 3, p. 15) states that a female of the same species, which was at least a young adult when first caught, lived 14 years in captivity. Ditmars (1919, p. 63) had an eastern diamondback (*C. adamanteus*) that lived 13 years and then died of an injury. Flower (1925, p. 977; 1937, p. 35), who compiled many records of the lives of animals in captivity, repeats Ditmars' record as the longest rattlesnake life known to him. The record at the London Zoo—held by a rattler of the same species—was somewhat under 11 years. Brimley (1942, p. 19; Davis and Brimley, 1944, p. 8<sup>o</sup>) mentions another eastern diamondback from Onslow County, North Carolina, that lived in the state museum for 14 years and

<sup>o</sup> Although the two statements do not agree exactly, I was advised by Dr. Brimley that they refer to the same snake.

9 months. It was adult when received, and was 4 feet 9 inches long at the time of its death. Loewen (1947, p. 53) tells of keeping a massasauga (*S. catenatus*) in captivity for 4 days less than 14 years. It was about a year old when caught.

At the San Diego Zoo, 20 rattlers have lived in captivity for 10 years or more, as shown in the accompanying table. It will be observed that two western diamonds (*C. atrox*) were still alive after 18 years in captivity, the longest-lived captive rattlesnakes known up to this time. One of these snakes was an adult when received, so that it was still alive at an age of not less than 21 years.

TABLE 6:2  
LIST OF RATTLESNAKES AT THE SAN DIEGO ZOO THAT HAVE LIVED MORE THAN 10 YEARS

Subspecies	Years	Months
<sup>a</sup> <i>C. adamanteus</i> .....	10	6
<sup>a</sup> <i>C. atrox</i> .....	18	0
<sup>a</sup> <i>C. atrox</i> .....	18	0
<sup>a</sup> <i>C. atrox</i> .....	17	7
<i>C. b. basiliscus</i> .....	10	1
<sup>a</sup> <i>C. c. laterorepens</i> .....	12	1
<sup>a</sup> <i>C. c. laterorepens</i> .....	12	1
<i>C. h. horridus</i> .....	15	7
<i>C. h. horridus</i> .....	11	11
<i>C. m. pyrrhus</i> ....	11	9
<sup>a</sup> <i>C. r. ruber</i> .....	13	3
<i>C. r. ruber</i> .....	13	2
<i>C. r. ruber</i> .....	12	3
<i>C. r. ruber</i> .....	11	1
<i>C. r. ruber</i> .....	10	1
<sup>a</sup> <i>C. tortugensis</i> ...	17	2
<i>C. unicolor</i> .....	13	6
<sup>a</sup> <i>C. v. helleri</i> .....	17	3
<sup>a</sup> <i>C. v. viridis</i> .....	15	7
<i>C. v. viridis</i> .....	12	2

<sup>a</sup> Still alive on June 12, 1954. As of October 12, 1955, the second and third *atrox* and the *adamanteus*, *ruber*, *helleri*, and *viridis* were still alive, so that 1 year and 4 months may be added to their records in the table.

Comparisons between the longevity of rattlers and other genera of snakes will be found in Perkins, 1948, p. 217; 1949b, p. 223; 1950b, p. 238; 1951a, p. 182; 1952, p. 280; 1953, p. 243; 1954, p. 229; and 1955, p. 262.

From these data, I should presume that rattlesnakes in the wild occasionally attain an age in excess of 20 years. Fitch (1949a, p. 538) in his study of the northern Pacific rattler, based on marked and recaptured snakes in the wild, reached the conclusion that these rattlers occasionally attain an age of 20 years, longer than either its prey or its competitive mammal and bird predators.

Much that is mythical has been published on the growth and longevity of snakes, rattlers included. Some of these ideas have evolved from certain ancient myths as to the great age that snakes attain because they are thought to renew their youth when they shed their skins. A common figure in these myths is 1,000 years (Jayakar, 1906-8, vol. 1, pp. 56, 634; Fayrer, 1892, p. 108; Corkill, 1932a, p. 609). Others stem from dual myths concerning some of the long strings of rattles which rattlers are said to acquire, together with the rattle-a-year theory. This, for example, explains

Bosc's statement (1803, p. 552) to the effect that rattlesnakes attain an age of 40 to 50 years. Meek (1946, p. 232) has absolutely no basis, beyond hearsay, for his claim of a diamondback 60 years old.

Ingersoll (1883a, p. 36) expressed the opinion that rattlesnakes mature in a single year, which has been shown to be contrary to fact.

### LIFE PERSISTENCE AND FRAILTY

It is popularly supposed that snakes—rattlers included—are highly tenacious of life. This belief is no doubt founded on the persistence of reflex body movements that continue long after a snake has been fatally injured, or even decapitated.

Probably the earliest statement as to the persistence of life in the rattlesnake was made by Hernández (1615, fol. 192<sup>v</sup>; 1628 and 1651, p. 329; repeated by Nieremberg, 1635, p. 269, and Jonstonus, 1653, p. 27), who reported that the head, if cut off, would live for 10 days or more. But such a theory, as applied to other snakes, is much older. Damiri, the Arabian naturalist, writing in the late fourteenth century (Jayakar's translation, 1906-8, vol. 1, p. 57), stated that if a viper be killed, the body will wriggle for 3 days; and the myth that an injured snake cannot die before sundown is both old and widespread. This was attributed specifically to rattlesnakes as early as 1722 (Beverly, p. 265). According to Bosc (1803, p. 553), Tisson dissected a rattlesnake that lived for several days after being virtually eviscerated.<sup>10</sup> Stories of decapitated snakes that lived several days were heard until quite recently (e.g., Lewis, 1874, p. 265). Lewis also reported that a decapitated rattler would retain the ability to strike for several hours.

Although these are exaggerations, it is true that there is a surprisingly long continuance of body movement in a decapitated snake, and that it is dangerous to handle the head of a venomous snake for some time after it has been separated from the body. Beverly (1722, p. 265) cut off a rattler's head. He let the head bite a stick, whereupon venom flowed from the fangs. Serious accidents have resulted from picking up severed snake heads or fatally injured snakes, and I wish to voice a warning against any carelessness in this respect. Staples (1865, p. 279) reported the case of a farmer, who, in mowing, cut off the head of a rattler. While brushing the grass aside to locate the head, he was bitten in the thumb with dangerous, but not fatal, results. Some two or three inches of the snake's neck had remained attached to the head. Anon. (1872, p. 46) recorded the fatal case of a child bitten by a decapitated snake in Ottawa County, Kansas. The snake's body had been severed three or four inches behind the head; it is not stated how the child happened to be bitten. Wolfe (1905, p. 351) called attention to the newspaper report of a fatal accident at The Geysers, Napa County, California, wherein a man was bitten by a northern Pacific rattler that had been shot into three pieces. Another case was reported in Santa Monica, California, in 1926. I was myself a member of a hunting party on which a man was bitten by a small southern Pacific rattler that had been shot in the neck with a .22 loaded with dust shot. Such a charge will break a snake's back and prevent it from crawling, but it will not be harmless until death

<sup>10</sup> The reference is evidently intended for Tyson (1683, p. 31); however, the snake therein mentioned was a European viper, not a rattler.

supervenes. As early as 1884, Ellzey (p. 250) had reported that the largest rattler could be killed with a few shot in the neck, which is true, but it should never be forgotten that a fatally injured rattlesnake is dangerous as long as any life or movement remains.

Ferrall (1832, p. 300) reported that a rattler's body squirmed for an hour after the head had been cut off. Harlan (1835, p. 503) stated that a decapitated head could bite, and that the body would strike with the stump of the neck. Gilman (1854, p. 26) beheaded a rattler with a hoe and observed that the neck would strike at anything that pinched it up to 1½ hours later. Among outdoor men generally, it has long been believed that if one decapitates a rattler, and the tail of the snake be pinched, the bloody stump of the neck will unerringly strike the hand of the pincher; and that no one has had the nerve to maintain his hold on the tail in the face of this fearful retaliation.

Some published accounts of accidents involving rattlesnake heads, after severance from the body, are as follows: Dugès (1877, p. 15), Clarke (1881a, p. 27), Cope (1892a, p. 687), Matteson (1899, p. 669), Backus (1903, p. 692), Dury (1910, p. 72), Menger (1913, p. 145), Maloney (1945, p. 80), and Allen (1949a, p. 72); see also p. 943.

#### EXPERIMENTS WITH DECAPITATED RATTLESNAKES

To determine the truth of some of these ideas, I experimented with 13 rattlesnakes of 6 different forms: a red diamond (*C. r. ruber*), a Mojave (*C. s. scutulatus*), 3 Great Basins (*C. v. lutosus*), 5 southern Pacifics (*C. v. helleri*), a southwestern speckled rattler (*C. m. pyrrhus*), and 2 Colorado Desert sidewinders (*C. c. laterorepens*). In no case was more than an inch of neck left attached to the head, and usually there was less than half as much.

Although I found a considerable variation in the actions of the decapitated snakes, I doubt whether any of the differences observed are to be attributed to species variations. The reactions of the notably placid red diamond seemed to be no less violent than those of the nervous southern Pacific. I presume that the differences observed in their involuntary actions are to be attributed largely to chance.

*Head Reactions.*—First, as to the head: I should say from this study that the head of a rattler, when separated from the body, is dangerous for at least 20 minutes, and sometimes for almost an hour. With only a short stub of neck, the head is, of course, quite immobile; any danger, therefore, must result from deliberate handling. True, in one instance (a southern Pacific), the head did hitch itself forward by digging the point of a fang into the table top and pulling on it, but this was certainly accidental.

The heads manifested continued life in various ways—by opening the mouth at the approach of a hand or other object, by biting a stick introduced into the mouth, by twitching the neck stub, by contracting the pupil of the eye, and by advancing and opening the end of the trachea or windpipe. Most of these reactions occurred only upon stimulation.

Unstimulated reactions, at least those not purposely stimulated—although some may have been caused by the movements of the observer—comprised skin twitching, opening the mouth, or twisting the neck stub. Skin twitching was most evident

at the angle of the mouth; it was observed as much as 19 minutes after decapitation in a sidewinder (*C. c. laterorepens*), and 29 minutes in the red diamond (*C. r. ruber*). Neck twisting is quite frequent and was noted even when there were only a few millimeters of the stump remaining. It was observed up to 20 minutes in a southern Pacific (*C. v. helleri*), and 28 minutes in a sidewinder. Some squirming is possible in the head itself and was occasionally seen.

The most conspicuous of unstimulated movements—or at least those not intentionally caused by the observer—was the opening of the mouth. Sometimes this was in the nature of a yawn, sometimes a biting threat with erected fangs. Generally, the movement was of progressively diminishing intensity after decapitation, as might be expected. The following instances were noted, the figures in parentheses indicating the elapsed minutes after beheading when the mouth was opened, together with other actions observed: sidewinder (1, 8, 11, 14, 16, 17; 18, fangs erected; 34; 40, gaped twice and partly closed, then opened wide; 44, partly opened), red diamond (10), Great Basin (5, 8, 13, 19, with the fangs advanced to the biting position in the last 2 instances), southern Pacific (13, fangs waved; 15, mouth opened very wide; 18, opened on one side). The sidewinder records for 18 minutes and more were all made by the same snake, which was outstanding in the persistence of its mouth movements.

From the practical standpoint of safety, any endeavors to bite by a severed head are of considerable importance. Tests were therefore made at repeated intervals by introducing a thin wooden rod into each snake's mouth. Positive reactions were noted in the following instances, the figures, as before, indicating the elapsed time in minutes subsequent to decapitation: Great Basin (2), red diamond (2, venom ejected), Great Basin (3, another specimen, venom ejected), medium southern Pacific (5, venom ejected), Great Basin (5 and repeated at 10 with venom ejection), large southern Pacific (7, a violent bite with much venom), another large southern Pacific (8, a relatively ineffective bite), sidewinder (10, venom ejected, fangs used separately), medium southern Pacific again (10, fangs used separately), Great Basin (12, a violent bite with venom ejected; repeated at 15), the other Great Basin (13, a violent bite with venom ejection, and the fangs manipulated separately), sidewinder (13, venom ejected), southern Pacific (17), Great Basin (20, not easily stimulated to bite, but finally bit hard), sidewinder (20, a strong bite when the stick was pressed inwardly against the angle of the mouth), southern Pacific (21, tried to bite, but rather ineffectively). At 43 minutes this same southern Pacific rattlesnake suddenly bit a stick that had been introduced behind the fangs, with a venom discharge. This was by all odds the longest delayed bite observed subsequent to decapitation. The jaw movement was certainly powerful enough to have imbedded the fangs in the hand and could well have caused a serious accident.

Decapitated rattlers do not always attempt to bite a stick introduced into the mouth; on the contrary they try as frequently to eject the stick without biting it. They do this by erecting and depressing the fangs, sometimes in unison, but often separately with a waving motion, as if to disengage them from interference, a manipulation that is quite characteristic when snakes are being milked of venom. Most of the snakes that would bite on some occasions would also try this maneuver on others, especially as they weakened. The southwestern speckled rattler was tested after 4, 17, 20, and 24 minutes and each time refused to bite, although it

always tried to void the stick. It was found that the best means of stimulating some reaction to an object placed in a snake's mouth was to press it back against the angle of the mouth, or against the mandibles. But even these annoyances usually failed to elicit further responses after periods varying between 15 and 30 minutes. However, it should be recognized that the exact time when the danger of a bite is definitely at an end is difficult to determine, for in some instances a specimen, after manifesting no response to stimulation, would suddenly react when the experiment was repeated several minutes later. I should say, as a result of these experiments, that most severed rattlesnake heads are probably dangerous up to 15 minutes, and possibly dangerous for three-quarters of an hour, or even more. As to a fatally injured snake, the duration of the danger would depend on the nature of the injury; the only safe rule is not to touch the head until the snake has actually begun to stiffen in rigor mortis.<sup>11</sup>

If the mouth be opened by elevating the upper jaw without introducing anything into it, the fangs are occasionally observed to wave or flutter in a vertical plane, one of the last movements manifested. This was observed in the southwestern speckled rattler up to 29 minutes, the Mojave at 33, and in 3 southern Pacifics up to 37, 39, and 40 minutes, respectively.

Various tests were made to determine the sense reactions in the severed rattler heads. The most positive was the pupillary contraction in response to a beam of light. It was found that, immediately after decapitation, the pupillary opening was about the same as in an uninjured snake under the same light intensity, and that the reaction to a flashlight beam was similar, but became progressively slower and less marked as death approached. Occasionally some twitching and eyeball rotation were observed. After death, the pupils remained dilated more than in bright light in life, with approximately a normal dim-light aperture. Two snakes, whose heads were rotated in a horizontal plane, exhibited the normal eyeball reaction described elsewhere (p. 389); that is, a lag in the directional change in the optical axis, followed by a compensating twitch.

Altogether, 57 eye-reaction tests were made on 12 specimens. To begin with, the pupillary reactions were well marked and rapid in all the snakes except the Mojave, in which the reaction was slow and slight even within the first minute. All others were considerable up to 10 minutes, after which a progressive decline in response was noted. However, two southern Pacifics still had strong reactions at 14 and 15 minutes, a sidewinder at 15, a Great Basin at 18, and the red diamond at 24 minutes. The final perceptible responses in those snakes that still reacted after 25 minutes were manifested by one Great Basin (out of three) at 28 minutes, one southern Pacific at 28 and another at 30 (out of four), the southwestern speckled at 30, the red diamond at 31, and finally one of the sidewinders at 30 and the other at 39 minutes. It should be understood that these final reactions were both slight as to the amount of pupillary contraction, and slow to become effective.

With decapitation, the control of the tongue seems usually to be lost at once. Sometimes the tongue was left partially protruded, but it appeared to be quite limp. Occasionally, in the effort to bite or to free the fangs from a stick, a slight

<sup>11</sup> The situation is somewhat different when snakes are being killed for preservation, by drowning in alcohol, by chloroform inhalation, or by similar means. The bodies must be preserved when limp, and one soon learns to recognize the sign—complete bodily relaxation—indicating that they can be safely handled.

inward or outward motion of the tongue was observed, but it seemed quite functionless and ineffective. Yet there were exceptions to this rule. In one instance a southern Pacific protruded and retracted the tongue immediately following decapitation. Again, at 2 minutes, this head was tapped on the top, whereupon the tongue was everted with the tips divergent, as in a live snake. The same response could not be evoked at 5 or 9 minutes, yet this snake was stimulated to protrude its tongue at 33 and 35 minutes, and the tongue was everted again at 39 minutes without stimulation. The tips were not spread in these later movements. Even at 41 minutes the head flinched when the tongue was pinched.

A Great Basin also showed a considerable tongue reaction. Immediately upon decapitation the tongue was everted and partially retracted several times; the tips were not spread. At 2, 3, and 4 minutes the tongue was repeatedly run out at the approach of the observer's hand. No reasons were apparent for the differences in the tongue reactions in these snakes, as compared with the others.

The glottis (terminus of the trachea, or windpipe), which lies just above the tongue sheath, was observed to be moving in most of the specimens, the motion being longitudinal, with the orifice opening and closing. In live snakes, when feeding, the glottis can be thrust forward to the edge of the mouth and beyond, thus furnishing an air inlet that will not be blocked, even when the mouth is distended to the utmost with food. No such extreme protrusion was observed in any decapitated snake, but some longitudinal motion was seen in a sidewinder up to 22 minutes, in a Great Basin up to 28 minutes, and in a southern Pacific—the one with the unusually tenacious tongue reaction—up to 35 minutes. The opening and closing of the orifice was even more persistent; it was observed at 27 minutes in the sidewinder and at 50 minutes in the southern Pacific. The latter, in fact, was the most protracted evidence of life exhibited in the severed head of this or any other specimen. There seemed to be some regularity of movement in the glottis: advance, open, close, retract, and then, after an interval, repeat.

A burning match was held near the facial pits of various specimens but no particular reaction was evident. Blowing the breath at the snout of the Mojave rattler at 18 minutes caused the mouth to open, but similar tests on other specimens failed to evoke any response. The red diamond flinched when a needle point was touched to a pit membrane, but this was not evident in a southern Pacific.

In a number of instances the approach of a hand, or even a finger, toward the snout caused the mouth to open and, in some cases, the fangs to advance. Here we have a reaction similar to that of a tethered rattlesnake; for although, contrary to repeated statements, an uninjured and free rattlesnake never threatens an enemy with open mouth, a snake that is held by the neck—in the venom milking process, for example—will do so. While no definite determination was made of the sense causing the mouth to open in the case of the severed heads, it was probably sight; the tongues were inoperative in all but one case, thus at least in part eliminating the sense of smell; and there was no evidence of intensified reaction to a match flame as might have been expected had the facial pits been the source of the reaction.

The open mouth in response to an approaching hand was by no means an invariable effect. Some of the snakes never did respond in this way; others would at times but not always. One small southern Pacific—the only one of the four of that subspecies to react in this manner—opened its mouth at an approaching hand

at 1, 4, and 7 minutes. The mouth closed again as the hand was withdrawn, showing clearly that the opening was caused by its approach. The response was weak at 7 minutes and was not repeated at 9. A Great Basin opened its mouth when the hand was moved above it at 4 minutes. In the red diamond there was no mouth opening at 3 minutes but a slight opening at 14. A sidewinder gave a positive reaction at 13 minutes. The best response was that of the Mojave rattler. At 2, 3, and 4 minutes it reacted quite violently, opening the mouth and erecting the fangs each time a hand approached, and closing the mouth as it was withdrawn. There was no response at 6 minutes, but again the mouth opened at 9.

External pressure on the head sometimes caused either flinching or such squirming as the neck stump was capable of. To rub the side of the head usually caused the neck stub to twist to the opposite side, a maneuver that would have caused the head to pull away, had the body been operative. Such a movement was evident up to 22 minutes in the red diamond. Touching the top of the head or pinching a fold of skin thereon usually caused the mouth to open. This was observed as late as 13 minutes in the red diamond and 16 minutes in one of the southern Pacifics.

Touching the severed spinal cord sometimes caused a violent reaction, generally evidenced by a gaping of the jaws with fangs advanced. This effect was demonstrated as late as 22 minutes in a Great Basin, although it was not repeated at 25. The reaction was accentuated when a probe was introduced longitudinally into the spinal cavity. However, in one instance, where the probe reached the brain, subsequent reactions seemed to cease earlier than was evident in other individuals, evidently from brain injury. When one head—a southern Pacific—was accidentally turned upside down, the neck stump squirmed as if to right itself.

*Body Reactions.*—The movements of the bodies after decapitation were more persistent but less functional than those of the heads. Whereas the longest evidence of life in a head was 50 minutes, movements of the bodies continued, although with interruptions, for several hours.

To test the ancient story<sup>12</sup> that the headless stump of the neck will always strike, with deadly accuracy, the hand that pinches the tail, every tail was immediately and violently pinched following the removal of the head. In none of the 13 instances did the promised action follow, nor was there even an approach to such a strike. The pinching usually caused a violent twisting or squirming, and sometimes there was a more or less accidental coiling about the hand, but it seemed to be quite fortuitous, without directional intent.

Nonstimulated reactions comprised an aimless and discontinuous twisting and squirming, gradually weakening and with progressively longer interruptions. Although these motions were usually evident in the posterior end of the body and the tail, the final motions could best be stimulated by a pinching of the neck and were evident anteriorly rather than toward the tail. It was found that stimulated reactions were most violent when the pinches engaged the spinal process or the dorsal scale rows.

In its reaction to pinching, the body often flattened itself as does an alarmed rattler, this being true of the posterior part of the body, or that near the part pinched.

<sup>12</sup> See, for example, Harlan (1835, p. 503), Mitchell (1860, p. 24), Catlin (1861, pp. 266, 268), Stejneger (1895, p. 380), and Brewer (1930, p. 189).

Two snakes that were rattling at the time of decapitation continued to do so for several seconds. No other snake ever rattled during the squirming period, nor did either of these two repeat.

In two instances, snakes that had been aimlessly squirming about, accidentally came up against sidewalls, following which they crawled along in the angle formed by the wall and the table, using a very slow rectilinear method of crawling. However, it should not be presumed that these were the only times rectilinear locomotion was in evidence, for there were others when the characteristic scale waves could be seen, although no progression resulted.

When held by one part of the body, the rattlers usually squirmed quite aimlessly but sometimes succeeded in wrapping the bodies about the hand that held them. In several instances the stump of the neck came to rest close to the restraining hand and pointing at it; but I cannot conclude that this was other than accidental, as it was by no means a consistent pose. In no case did the stump strike or even press against the hand.

I have elsewhere discussed the sensitivity of the ventral surface of the body to vibration (p. 395), an effective substitute for the sense of hearing, which snakes lack. One of the most interesting developments of these experiments was the evidence that the headless bodies were susceptible to vibrations of the substratum, for the bodies could be caused to squirm when previously they had been still. These responses were, it is true, observed in somewhat less than half the tests made, and it required a rather sharp vibration of the table to produce them. Such reactions were observed on the speckled rattler at 8 minutes, on one of the Great Basins at 15, on a sidewinder at 17 and 20, and on one of the four southern Pacifics at 10, 19, and 34 minutes.

Another interesting reaction was the ability of the bodies to right themselves when turned on their backs. Again the results were highly variable, for sometimes they would turn immediately, at others only after an interval; again, they had to be stimulated to squirm before they would turn, and in some instances they would make no effort even when annoyed. One Great Basin righted itself at 4 minutes, but failed to do so at 14, 20, or 47 minutes. Another Great Basin righted itself quickly at 3 hours, and again, this time with a little stimulation, at 3 hours and 35 minutes. Left on its back, this snake suddenly righted itself without stimulation 5 hours, 2 minutes after decapitation. The third Great Basin, after lying on its back for 15 minutes, suddenly righted itself without stimulation; this was 20 minutes after decapitation. This snake quickly righted itself when turned on its back at 28 minutes. One sidewinder righted itself with stimulation at 18 minutes. The Mojave rattler quickly turned over at 26 and 40 minutes; it repeated at 1 hour, 12 minutes, but only with stimulation to start its movements. The red diamond, at 13 minutes, righted itself only after being on its back for about a minute. The southwestern speckled rattler righted itself quickly at 5 minutes, failed to do so at 13, and turned over, with outside stimulation to initiate motion, at 22 minutes. One large southern Pacific made no attempt to right itself at 12 minutes but suddenly did so without stimulation at 13. The most surprising feat was that of a southern Pacific rattler that had been on its back for some time. At 7 hours and 43 minutes after decapitation, its tail was pinched and it righted itself immediately.

Spontaneous body squirming without stimulation lasted at least 2 hours with all but one of the snakes; and more than half exceeded 4 hours, including a young southern Pacific (4:29), a large southern Pacific (4:46), one Great Basin (4:56) and the other (5:02), a large southern Pacific (5:55), the red diamond (6:35), and another large southern Pacific (7:26). Although the final voluntary movements were usually observable in the tail or at least the posterior part of the body, the final stimulated motions could usually be evoked by pinching the neck vertebrae and were in the neck itself. The records of the elapsed times following beheading at which motion could still be evoked by pinching, were as follows, the figures representing hours and minutes: sidewinder (2:45), southwestern speckled (3:29), southern Pacific (4:46), Mojave (5:00), small southern Pacific (6:20), large southern Pacific (6:37), Great Basin (6:38), red diamond (7:18), Great Basin (7:22), sidewinder (8:13), large southern Pacific (9:13). Observations were not recorded on two of the snakes. The temperature during these tests varied from 20° to 22° C. (68° to 71½° F.).

It will be observed that none of the figures approaches those that some travelers have reported. On the other hand, there have been reports of immediate cessations of movement that are equally hard to credit. Wallace (1950, p. 116) reported the shooting of a very large eastern diamondback. Within 5 minutes it had ceased to twitch and could be measured. This is even harder to believe than its length of 8 feet 4 inches.

In none of these tests were the anal scent glands discharged. William H. Stickel has written me of a western diamond rattler (*C. atrox*) that was shot in the neck, a few pellets from a .22 shot-shell taking effect about two inches behind the head. Anteriorly the snake seemed to be quite helpless, but the body and tail responded to stimulation. An hour or two afterwards there was a discharge of musk when the tail was touched; this was repeated several times, which shows it was not fortuitous.

*Persistence of the Heart Action.*—As a final evidence of the persistence of the life force in rattlesnakes—as in other snakes—there is the matter of heart beats, for the heart continues to beat, not only for a long time after decapitation, but long after the body has ceased to move even when pinched. The experiments that I made were performed after the end of the observations on bodily movements. At that time the snake was turned on its back and a slit was made in the abdominal wall just above the heart, so that its beating could be seen.

The heart beats at first at a rate of about 45 per minute, which seems to be normal for a live rattlesnake, and then, after decapitation, gradually declines to a rate of 3 or 4 per minute. But this decline is not uniform. On the contrary, there may be a drop to 15 or 18, and then, a few hours later, the rate may have climbed again to 24. But gradually the pulse both slows and weakens, until finally it can be seen no more. Usually the ventricular beats are affected first; in some instances, toward the end, there were 2 to 3 auricular beats to each ventricular. Also, there is an increasing irregularity, so that the beats are by no means evenly spaced. Without doubt my experiments have been affected by the snakes' condition and the nature of the incision. Some terminations seemed the result of desiccation.

Eliminating the specimens whose heart actions ceased during relatively long

periods without observations, we have the following approximate durations of heart activity subsequent to decapitation, the figures being given to the nearest even hour: sidewinder (15), Mojave (18), southern Pacific (30), southern Pacific (31), southern Pacific (45), Great Basin (46), Great Basin (50), and sidewinder (59). In no case was the heart actually seen to stop; and as the elapsed times have been given to the last observed beat, some of these figures may be from one to as many as 8 hours low, depending on the frequency of observations. But it is demonstrated that the heart usually beats for at least one day in a decapitated rattlesnake, and in some instances reaches and even exceeds two days. Toward the last the beats are little more than pulsing waves in the heart muscle.

*Conditions Favoring Persistence of Movement.*—The persistence of reflex movements in snakes and other reptiles arises in some degree from the relative importance of the brain and the spinal nervous centers, for the spinal centers are of greater relative importance in the reptiles than in birds and mammals. But in addition it should be pointed out that in the reptiles there is no sudden fall of temperature coincident with any interruption of the metabolic processes, the oxygen requirements are lower, and therefore nerves and muscles may continue to function in what is, for them, a normal temperature and almost normal environment. Indeed, heat may not prolong movement. An observer (H. H. in Bevan's "Snake Lore Column," *Outdoor Life*, vol. 68, no. 2, p. 78, Aug., 1931) reported that when the heads were shot off two rattlers, one body being left in the sun while the other was placed in the shade, that in the sun stiffened first.

#### BODILY FRAILTY OF SNAKES

Despite their seemingly strong hold on life, as indicated by the persistence of movement in these decapitation tests, snakes—rattlers among them—are relatively frail creatures and are easily killed, although this statement should not be interpreted as calling in question the dangerous character of poisonous snakes as long as capacity for movement continues. This frailty stems from the fact that their backbones are both delicate and vulnerable, so that a smart blow of no great force will produce a fatal injury, although at first it will seem to interfere only with locomotion. Audubon (1827, p. 29), Tixier (1940, pp. 76, 208, written in 1840), and Rollins (1922, p. 178) have noted how easy it is to break a rattler's back. Thus, it is probable that most snakes run over on the highways are usually fatally injured, however successful they may be in squirming off the road. As an example, I may cite a southern Pacific rattler that I found by the side of the road in what appeared to be a stunned condition. It was placed in a cage, where it quickly became lively again and seemed to be enjoying good health. Two weeks later it was killed and preserved, and upon the opening of the peritoneum the major organs were found suffused with blood and even the heart appeared damaged. Certainly this snake would have died within a short time. Had its back been broken by the car that struck it, survival for more than a day or so would have been improbable.

Occasionally there are recoveries from what seem to be fatal injuries. From time to time one will find a live rattler with its rattles cut off and scars on the head or body that mark the site of healed injuries. Clearly these snakes had been "killed" and the rattles removed as trophies, yet they had survived.

Some writers (e.g., Fountain, 1906, p. 303; Berridge, 1926, p. 25; Crites, 1952, p. 65) have mentioned how quickly a snake can be disabled by a blow on its tail, leaving the inference that the tail is even more vulnerable than the body itself. This is certainly not true of rattlers, with their shortened tails; and probably is not true of any snakes, judged by the frequency with which snakes with attenuated tails, such as the racers *Masticophis* and *Coluber*, for example, are found alive in the wild with much of their normal tails missing. Probably this idea of the particular vulnerability of the tail is the outgrowth of a misunderstanding of just where a snake's body ends and its tail begins. No doubt a broken spine anywhere on the body itself will be fatal, although not always immediately.

Snakes do not regenerate their tails as do most lizards. The myths of the glass snakes and other snakes, to the effect that, when cut to pieces, they are able to reassemble themselves, are based on certain legless lizards that can lose a surprisingly long stretch of tail, and live to go about their business with the body intact and uninjured. An early form of this myth was published by Roger Bacon (Thorn-dike, vol. 2, 1923, p. 656). The loss of the tail in lizards is a more usual and natural event than in snakes, for many kinds of lizards have tails that may be detached—at any one of many parting-planes—as a result of the slightest blow or effort of detention. This is a defense mechanism of a highly successful character; for many a lizard enemy finds himself in possession of a lively, squirming lizard-tail, while the creature itself has escaped to grow another.

There is a story going the rounds which, in its most extreme form, is no doubt mythical, but which may have some factual basis. Ludwick (1930, p. 121) tells of a man who opened a bale of hay that had been baled two years before, and found in it a live rattler. The press services carried a story on September 9, 1953, that told of a live rattler found with eight inches of head and neck protruding from a bale of hay. As no duration of imprisonment was given, this one may have been authentic.

### SKIN SHEDDING

Rattlesnakes, like other snakes, shed their skins periodically. This shedding—exuviation, ecdysis, or desquamation are alternative terms—is an important requisite to the health of the snake; presumably it is necessary to provide for both growth and wear. It is known that young snakes shed more frequently than adults, from which it may be presumed that the requirements of growth in the juveniles take precedence over the necessity of replacing a worn skin. However, it should be understood that this is a matter of correlation, rather than one of proven cause and effect.

Elsewhere (p. 302) it has been shown that a rattlesnake adds a rattle to the string each time the skin is shed. Thus, where an unbroken rattle string is in evidence, we have a record of the number of sheddings since birth, for the disclosure of the No. 1 rattle—the button—is coincident with the first shedding, at which time the prebutton is lost. Much of the data on shedding intervals is deduced from the rattles.

## SYMBOLISM AND FOLKLORE

Various interpretations of the reasons for the skin-shedding process of serpents have entered into the mythology of many races. Krappe (1930, pp. 61, 256) states that the belief that snakes are immortal, through their ability to restore their youth by acquiring a fresh skin, is world-wide, and is usually connected with some story of the fall of man, for immortality—originally man's possession—was stolen from him by the snake. Immortality through shedding is mentioned by Aristotle (Cresswell, 1862, p. 121); Rendell (1928, p. 12) finds it in Theobald's *Physiologus*<sup>13</sup>; Calmet (1812, vol. 2, art. Serpents) quotes it from Epiphanius' *Physiologus* of about the fourth century; de Wet (1929, p. 1036) mentions it as a Hindu belief; and Budge (1930, p. 489) comments on its ancient derivation.

Most modern folklore with regard to skin-shedding has to do with the frequency of the process and its seasonal regularity; the degree and duration of the blindness incurred; and the effects on the snake's disposition. These ideas will be discussed in connection with particular phases of the shedding process.

## SKIN STRUCTURE

The histology of the rattlesnake skin has been described by Rahn (1941, p. 229), Lynn (1931, p. 113), Zimmermann and Pope (1948, p. 386), and G. H. Parker (1948, p. 210). Rahn pictures the skin as being composed of two layers—an inner, thicker one, the dermis; and an outer, thinner epidermis, which, in turn, is itself divided into two layers, a *stratum germinativum* next to the dermis, and, outermost of all, a *stratum corneum*. The *stratum corneum* comprises completely keratinized and flattened cells, and is destined to be discarded at the next shedding. After shedding, the outer cells of the *stratum germinativum*, pushed outward by younger cells below, begin, themselves, to flatten and keratinize until, once more, a *stratum corneum* has been formed. The process of keratinizing involves a deadening and hardening of the cells, thus forming a skin partially impervious to moisture, and resistant to corrosion and wear.

It should be understood that this periodical shedding and replacement of an outer wearing surface is by no means a unique procedure of the snakes; on the contrary, it is characteristic of almost all land vertebrates. In most animals, however, the process is more gradual and continuous, and consequently less conspicuous; even in the snakes' nearest relatives, the lizards, desquamation usually involves the loss of the skin in patches. But in a healthy snake, when the time arrives, the *stratum corneum* is shed in a single, unbroken piece, representing every exterior part of the snake, from the edge of the lips to the tip of the tail. Even the outer layer of the transparent scale over the eyeball is shed; and, in the rattlesnakes and other pit vipers, the surfaces of both the anterior and posterior chambers of the facial pit are evident as tiny bags attached to the skin. Nowhere are the remarkable structural continuity and chronological uniformity of the shed skin more in evidence than in the presence of the bags representing the posterior pit chambers; for these are attached to the rest of the skin only by thin stalks that comprise the inner surfaces of the tiny tubular orifices which give access to the posterior chamber. In shedding, these interior surfaces are pulled through the orifices.

<sup>13</sup> The *Physiologus*, a series of allegories attributed to the various authors who transcribed them, dates back at least to the second century, A.D.

The shed skin is translucent and straw-colored when clean; however, it is usually darkened by foreign matter to a brownish color. It is often possible to discern the snake's pattern as a slight, or even strong, darkening of appropriate areas, but the color and pattern are largely retained by the *stratum germinativum* and the dermis, now more brilliant than ever since the cells carrying the color are unmarred by hardening or wear, and are nearer the surface.

TABLE 6:3  
THICKNESSES OF SHED RATTLESNAKE SKINS  
(Averages of five skins shed by 5-foot 11-inch snakes.)

Scale covered	Thickness, mm.
Rostral . . . . .	0.069
Prenasal . . . . .	0.053
Pit lining . . . . .	0.018
Upper preocular . . . . .	0.030
Genial . . . . .	0.051
Gular . . . . .	0.048
Eye cap . . . . .	0.051
Between dorsals <sup>a</sup> . . . . .	0.023
Laterals . . . . .	0.043
Between laterals . . . . .	0.030
Ventrals	
Anterior	
leading and trailing edges . . . . .	0.051
lateral ends . . . . .	0.053
center . . . . .	0.076
Mid-body	
leading and trailing edges . . . . .	0.051
lateral ends . . . . .	0.058
center . . . . .	0.114
Near anal plate	
leading and trailing edges . . . . .	0.038
lateral ends . . . . .	0.051
center . . . . .	0.071
Subcaudals, center . . . . .	0.056

<sup>a</sup> The dorsals themselves are too irregular and striated to permit accurate measurements.

Despite the fact that the skin is shed in a single piece, it is delicate and frangible, with little tensile strength. Such a shed skin should not be confused with the durable and ornamental snakeskins whose commercial uses are described elsewhere (p. 1057). These commercial skins include the entire epidermis and the dermis as well; the snakes must be killed to secure them.

The scales of snakes are not separate, removable parts as they are in most fishes; on the contrary, they are formed by folds in the skin, just as a roof might be formed of a single unbroken sheet of material so folded as to give the impression of separate shingles. Since the *stratum corneum* covers not only the tops of the scales, but follows the folds beneath and between them as well, it comes off as an unbroken sheet. The scales are by no means haphazard in arrangement, but fall into regular patterns both on the head and body. These patterns of arrangement are quite consistent within subspecies and are extensively used in classification (p. 195). Specimens that are badly preserved, or allowed to dry before being returned to the preservative, will often lose the *stratum corneum* that forms the tops of the

dorsal scales, which might lead one to presume that the scales are actually separate, rather than being formed only by the folding of the skin. Whether there are differences between the skin of scale tops and that covering the spaces between, other than obvious differences in thickness, will require further histological researches to determine.

To ascertain the variation in the thickness of the several parts of a normally shed *stratum corneum*, four skins from two large western diamonds (*C. atrox*) about 1,800 mm. (5 ft. 11 in.) long, and one from an eastern diamond (*C. adamanteus*) of the same size, were examined and the thickness of the skin determined. Considerable variations in thickness were observed, as shown by table 6:3 giving the averages of the 5 skins.

TABLE 6:4  
COMPOSITION OF KERATINS IN PER CENT  
(All determinations were made on a moisture-free basis)

Substance	Rattle	Rattlesnake skin	Cattle horn	Human hair
Carbon .....	47.33	48.17	50.89	48.14
Hydrogen.....	7.17	6.94	6.72	6.89
Sulphur.....	1.35	1.13	3.17	4.12
Nitrogen.....	14.13	13.08	16.66	16.06
Ash.....	2.53	9.12	0.40	0.74
Difference (Oxygen, etc.).....	27.49	21.56	22.16	24.05

As indicated by these measurements, the skin covering the ventrals is thickest at the center and tapers toward the edges; the taper is so rapid that the measurements at the leading and trailing edges are not entirely accurate. The folds at the trailing edges of the ventrals are sharp and knifelike; the skin, as doubled at this point, about equals the thickness of the single layer at the center of a ventral, where it is thicker than anywhere else on the body. Everywhere the skin thickness seems to be related to possible wear and to necessary scale strength. The eye covering is quite stiff and strong, partly owing to the dome effect. The skins of a pair of 3-foot northern Pacific rattlers (*C. v. oregonus*) that had shed naturally in the wild were found to have approximately the following thickness in millimeters: center of ventral plates at the neck 0.055; ventrals at mid-body 0.071; ventrals anterior to the anal 0.050; lowest laterals at mid-body 0.043; mid-dorsal 0.033. The measurements of the dorsals and laterals are hardly trustworthy, since the pieces to be gauged were small and irregular. One mid-ventral fold was flattened and found to measure 0.056, compared with 0.069 mm. at the center of the adjacent ventral. It should be understood that all of these thickness measurements are approximations, owing to the compressibility of the material.

Keratin, of which the shed skin of a snake is comprised, is defined as "an albuminoid forming the chemical basis of epidermal tissues, as horn, hair, nails, feathers, and the like, and existing apparently in several varieties" (*Webster's International Dictionary*, Second Edition). C. E. White of San Diego made chemical analyses in duplicate on keratin derived from several sources, with the results shown in table 6:4, all components being expressed as percentages.

The high ash content of the skin is notable; it was found to contain iron, calcium, magnesium, aluminum, manganese, potassium, sodium, phosphates, sulphates, chlorides, and silica.

Shed snake skins are readily eaten by clothes moths and by ants.

It has been found that when snakes are caused to shed prematurely, which is likely to occur when they have been overheated, much more of the color and pattern is observable in the shed skin than is normally the case. Evidently either some of the *stratum germinativum* is carried away with the *stratum corneum*, or the reduction of the melanin through keratinization or retraction back into the lower layers is incomplete.

The division of the skin of a snake into separate scales has a number of advantages. The ventral plates may be of some assistance in certain of the types of locomotion employed, through the ratchet effects of their sharp trailing edges, as is discussed elsewhere (p. 368). Probably the folds serve to add mechanical strength by doubling the thickness on scale edges and also through the reinforcement of the ridges. But no doubt the most important advantage lies in the increased flexibility and the degree of stretching that the interscale-skin permits. This can readily be seen when a snake is distended with food or eggs, for at such times the interscale folds are flattened and the space between scales increased. This expansibility also facilitates bodily movement. Likewise, it must be remembered that the system of scalation aids in the skin-shedding process itself, for when the folds are flattened, the entire skin is materially enlarged, and so it is that the relatively narrow skin at the neck can be pulled back, without difficulty, over the much thicker body.

Rattlesnake dorsal scales are keeled—that is, there is a longitudinal ridge down the middle of each scale. These keels are absent on the lowest one to three scale rows on either side. Walls (1938, p. 103) has suggested that the keels may have an adaptive advantage in reducing shininess, that otherwise might lead to discovery by enemies. In some rattlers, particularly those of Central and South America belonging to the species *Crotalus durissus*, the keels are especially conspicuous, for they are widened just posterior to the middle of each scale into a prominence, or boss, that gives these snakes a particularly rough-scaled appearance. The ridges probably serve as longitudinal reinforcements; they may also affect reflectivity or heat absorption from radiation. The dorsal scales are also striated, with small auxiliary ridges radiating posteriorly from the central ridge.

Many snakes have tiny pits—the so-called apical scale pits—at the posterior end of each scale, single in some genera, paired in others, as is usually the case in those with keeled scales. In some snakes the scale pits are quite prominent, but in the rattlers they are only faintly evident as a pair of minute indentations at the posterior tips of some of the dorsal scales. They are more apparent toward the tail or on the tail. A few rattlesnakes, including the Neotropical rattler (*C. durissus*), the speckled rattler (*C. mitchelli*), the massasauga (*C. catenatus*), and their subspecies, have more prominent pits than others. In some forms the scale pits are accentuated by dots of color; this is particularly true of the Aruba Island rattler (*C. unicolor*). The purpose of the pits—and the skin glands of which they form the orifices—is still uncertain. Some have thought they might have a connection with skin-shedding; others have associated them with scent in sex recognition or with some tactile function. Pits are shown on the scales above Nos. 9 and 10, fig. 2:64.

The rattlesnake's skin, even with its keratinized outer layer, is not completely moisture-proof, and snakes can suffer serious desiccation.

#### THE SHEDDING OPERATION

A healthy snake sheds its skin by crawling through it in such a way that the skin peels backward over the snake's body, turning inside out as it proceeds. It is like peeling a glove off a finger, the base of the finger representing the snake's head, and the point of the finger its tail.

The snake about to shed shows some nervous activity. Finally it rubs its snout on some rough object, thereby loosening the old skin along the edges of the upper and lower lips. Then the coverings of the top and lower surfaces of the jaws are loosened and turned back over and under the head. More scraping or rubbing against rocks or shrubbery, together with skin movements, and body kinking and writhing, continue the process, pushing the old skin back over the body. A healthy snake needs no external object against which to shed, although it will use one if available. A snake enclosed in a glass jar has been seen to shed by scraping one part of the body against another. Sometimes there may be a temporary impediment and the old skin will gather into a bunch of accordion pleats. But soon this difficulty is surmounted, and, once the narrow neck-section has passed over the thickest part at mid-body, the snake quickly crawls, using rectilinear progression, through the remaining part of the skin and finally emerges with its bright, fresh surface fully disclosed. The old skin, sometimes bunched, but more often fully extended and inside out, is left to be destroyed by the elements or to be used as nest material by some fearless bird.<sup>14</sup> Many kinds of lizards, and a few snakes, are known to eat their shed skins, but this is not the practice of rattlesnakes.<sup>15</sup>

The normal shedding process requires from a few minutes to several hours, depending on the health and activity of the snake, the temperature and humidity, the availability of rough objects on which to scrape, and similar conditions. Snakes in poor health, especially when afflicted with external parasites, sometimes have great difficulty in shedding, although the shedding, if complete, helps to eliminate the pests. Often the skin comes away in patches, trouble being had particularly with the eye caps. No doubt such difficulties are of more frequent occurrence in captivity than in the wild. Some of the inaccurate beliefs respecting shedding have been initiated by observations of nonnormal individuals adversely affected by captivity.<sup>16</sup> But caged snakes that are well cared for and free from mites have no difficulty in shedding. C. B. Perkins of the San Diego Zoo reports that his charges, including the rattlers, nearly always shed the skin in one piece, and that they have little trouble in starting the process at the lips.

The shedding mechanism is not a simple matter of brushing off a worn skin:

<sup>14</sup> For lists of birds using snake sloughs as nesting material, see Strecker (1926c and 1927b) and Grant (1948).

<sup>15</sup> Occasionally a recently shed skin is the means of locating a concealed snake. Charles H. Lowe, Jr., told me of finding a pair of eastern diamondbacks (*C. adamanteus*) in Florida when a snake skin in the open caused him to search nearby places of concealment. The shed skin was 6 feet 1 inch long, whereas the larger of the two snakes was one foot shorter. This shows the increased length resulting from the shedding processes and the straightening out of the folds between scales.

<sup>16</sup> There is a general belief that healthy European vipers shed their skins in patches. This, for example, is stated by Leighton (1901, p. 70), but is denied as being mythical by Elliot (1934c, p. 276).

rather, it involves various physiological provisions facilitating the process. Bruner (1907, pp. 87, 92) has described a mechanism whereby reptiles can raise the venous blood pressure in the head. This serves as an aid to exuviation by swelling the head and loosening the skin. It was observed in the eastern diamondback rattler (*C. adamanteus*), among other kinds of snakes, and is no doubt utilized by all rattlesnakes. Fraser (1936-37, p. 78) observed that snakes often yawned to start exuviation at the head; and Hudson (1947, p. 69), describing the shedding of a young sand viper (*Aspis vipera*), mentioned the fact that the snake opened and closed its mouth, and that the labial plates were moved as if to expedite the loosening of the slough at the lips. These observations by Fraser and Hudson may well be the external manifestations of the blood-pressure rise investigated by Bruner. Sometimes a snake is seen to move or bulge the scales of the skin at the part of the body where the old slough is being detached; this is particularly evident at the lower lateral plates where the movement is somewhat like that used in rectilinear locomotion. The late Mrs. Grace Olive Wiley had an excellent moving picture of a western diamond rattler shedding its skin. The old skin was seen to be loosened by a rippling or caterpillar movement produced by the subsurface muscles at the point where it was being turned back. These movements caused the old skin to become loose scale by scale, and the snake crawled through it, turning it inside out as it moved, without making any attempt to brush the skin against an extraneous object or to hold it down with its own body. Gibbs (1892, p. 7), watching an eastern massasauga (*S. c. catenatus*) as it shed in the wild, claimed that it loosened the skin by swelling the body with air. Corkill (1932b, p. 2) states that exuvial glands aid in the shedding, presumably by discharges that loosen the *stratum corneum* from the layer below. It is this discharge that causes the characteristic milky or bluish appearance of the eye of a snake sometime before the shedding; it may also be seen at the proximal rattle of a rattlesnake. Although the exudate clears some days prior to the actual shedding, a fresh slough will be found quite moist, as was noted by Garman long ago (1888, p. 259; 1889, p. 172).

#### EFFECT OF SHEDDING ON SIGHT

The skin-loosening discharge is exemplified, at a certain stage of skin shedding, in the exudate that appears between the new and old covering of the eyeball of a snake—the well-known “blue-eyed” stage that causes partial blindness, but which clears up some days before the actual shedding takes place (Garman, 1889, p. 171; Metcalfe, 1907, p. 123; Pitman, 1938, p. 10; Davenport, 1943, p. 18). Many have thought that the blindness is caused by a thickening and resulting opacity of the old skin, but this is not true, as is evident from the fact that the eye clears again before the old skin is shed. Garman noted this as early as 1893 (p. 102), for he observed that the cloudiness of the eye of a shedding timber rattlesnake (*C. h. horridus*), which became apparent beginning on August 17, disappeared on August 30, although the snake did not shed until September 4. In a massasauga (*S. catenatus*) the milky appearance began on September 12 and had cleared away by September 19, and the snake shed 5 days later. In another snake of the same species, the interference vanished 8 days before shedding. Garman also observed that the milkiness lasted longer in specimens kept in the shade than those in the sun, indicating the clarifying effect of drying. He observed the same opacity in the

snake's proximal rattle sometime before shedding. Storer and Wilson (1932, p. 169) noted a northern Pacific rattler (*C. v. oreganus*) in which the opacity cleared 6 days before shedding.

C. B. Perkins at the San Diego Zoo made observations of 21 skin-shedding schedules of the rattlesnakes of 9 different subspecies, recording the onset of blueness in the eye, the peak of opacity, the day of clarification, and the final interval before shedding. The data may be summarized thus: The interval between the onset and the peak of blueness varied from 2 to 7 days, with an average of 3.8; the period between this peak and the time when the eye cleared up again varied from 1 to 7 days, with an average of 4.3 days; and, finally, the elapsed time between clarification and shedding ranged from 2 to 6 days, with an average of 3.7 days. This final figure is probably the most objective of the series, since it is easier to determine when the eye has cleared than when the peak of blueness is attained. Taking the start of opacity as an indication of the beginning of the shedding sequence, one can see that the average duration (to the final shedding) of this critical period in the rattlesnake's life, in these captive specimens, was 11.8 days.

Jackley (1946a, p. 2) has expressed the belief that rattlers with their vision impaired by incipient exuviation are seldom seen abroad, but stay down holes or in other refuges. There is little doubt that this is true, for a snake would be less active when suffering the discomfort of partial blindness, and would be less likely to expose itself to its enemies while lacking the full use of one of its senses.

The scale that covers the eyeball is quite clear in a shed skin—clearer, in fact, than any other element of the skin. This is a further proof that the opacity is not caused by a change in the skin itself.

#### WATER REQUIREMENTS DURING SHEDDING

Mitchell (1860, p. 4) stated that rattlers are especially in need of water at shedding time. Pope (1925b, p. 130) expressed the belief that when a rattler sheds in patches lack of water is the probable cause. Quelch (1891, p. 8) noted that captive Neotropical rattlers (*C. durissus*) drank more water before skin-changing, and were likely to stay on the ground, when at other times they climbed the branches in their cages. Fraser (1936–37, p. 78) observed that snakes having difficulty in shedding, took to the water; and King (1941, p. 58) thought they shed more frequently in rainy weather. C. B. Perkins believes that healthy snakes can shed equally well with or without water available. However, if one has difficulty in shedding, exuviation can be facilitated by putting it to soak in water for a night. K. P. Schmidt informed me of a captive sidewinder whose condition became so bad that it was decided to destroy it. For this purpose an attempt was made to drown it in warm water. The following morning it was found to have shed several layers of skin (about five), and this was followed by its recovery, so that it lived for some time thereafter.

Benedict (1932, p. 122) found that the onset of the shedding process in snakes led to an increased loss of water by evaporation through and from the skin. Bogert and Cowles (1947, p. 1) made tests tending to verify this observation. They are of the opinion that snakes seek water during ecdysis to avoid desiccation, and not to loosen the skin (p. 24).

## RATTLE ACQUISITIONS

It is now well known that a rattlesnake acquires a new rattle each time the skin is shed, the homology of the rattle with elements of the skin being recognized. The belief has been expressed (Kunzé, 1879, p. 333; Smith, 1882, p. 672) that the fang replacement is also coincident with shedding, but this lacks confirmation.

## THE SEASON OF SHEDDING

There are various folklore beliefs regarding the mechanism of skin changing. Pliny (1855-57, vol. 2, p. 292; Thorndike, 1923, p. 74) stated that snakes eat, or rub themselves with, fennel preparatory to shedding. Brendle and Unger (1935, p. 200) record the belief of the Pennsylvania Germans that snakes shed by using brier thorns as hooks wherewith to pull the skin off. Tome (1928, p. 114, but writing in 1854) thought the rattler's skin loosened at the tail first. But much of the recent folklore concerning shedding has to do with the seasonal regularity of shedding and its effects on the habits and dispositions of the snakes. I have discussed elsewhere (p. 459) the almost universal belief that rattlesnakes are blind—from the preparation for shedding—in August, and, at that time, are particularly dangerous.

As a matter of fact, there is little evidence that the snakes adhere to a rigid chronological schedule in changing their skins. Probably the weather, success in capturing prey, and other variable conditions tend to change, at least to some extent, the elapsed time between exuviations. This variation has been noted in captive specimens that are kept under more uniform conditions than exist in the wild. Messeling (1953, p. 22) expressed the opinion, not corroborated by any records, that *horridus* sheds once a year, unless there is a wet spring, in which case it sheds twice. Certainly in the young, which change their skins more frequently than adults, the effect of the food supply is readily noted; for in the juveniles the periods of successive skin changes are correlated with growth rather than with age, and growth is dependent on food. Sometimes certain young snakes in a brood will accept food when their brothers will not, and their more rapid growth and more frequent skin-changing become quite apparent. This is further verified by the conclusion from growth studies that the larger snakes in any single age-class have more rattles than the smaller. Thus it is clearly seen that the frequency of shedding is correlated with size rather than with age alone.

It is true that there is one ecdysis that runs quite true to schedule—that of the young rattlesnakes after birth. As indicated elsewhere (p. 730) this usually occurs from 7 to 10 days after birth.

If there is any other regular shedding time, it probably follows immediately upon emergence from hibernation. This was suggested long ago by Aristotle (Creswell, 1862, p. 216). Volsøe (1944, p. 17) has found this to be true of the European vipers; and it may indeed be the case with those rattlers that dwell in areas having long cold winters, and, therefore, relatively short active seasons. Further studies on this matter of seasonal regularity are desirable.

One myth has it that rattlers shed annually for 7 years and then shed no more. Grant Watson (1937, p. 210) relates this story: A large venomous black snake was killed in Tasmania, and the skin was mounted and sent to England, where it was

hung on the wall of a dining room. Every year for the next 10 years it shed a thin gauze-like skin of outer scales. Can this be another of those gratuitous criticisms of British cooking?

#### SHEDDING FREQUENCY

Coming now to the intervals between exuviations, as differentiated from the season of skin-changing, I must admit that much of our available information is of somewhat doubtful validity, based as it is on observations of captive specimens. There is no denying that the conditions of captivity seriously modify the shedding schedules, particularly because of the maintenance of relatively high temperatures in the reptile houses during winter. But even so, we can at least show that the growing young shed more frequently than adults, as was suggested by Ingersoll (1883a, p. 37). Further, because the rattles themselves are records of desquamations, we are able to assemble the statistics of unbroken rattle strings and gain some idea of the natural sheddings in the wild during the first year or two of life.

For example, most of the prairie rattlers (*C. v. viridis*), having unbroken rattle strings when found at the hibernating dens, have either 1 or 5 rattles; few have 2 or 4, and almost none has 3. Those with one rattle, the button, are obviously young-of-the-year, while 5 evidently represents the mode for the next age-class. This means that these snakes, at an age of about 16 months—about 7 or 8 months of actual activity—have changed their skins 5 times, if we include the change immediately following birth, when the prebutton was shed and the button disclosed. Similar studies of the southern Pacific rattlesnake (*C. v. helleri*) and the red diamond (*C. r. ruber*) in San Diego County, California, indicate 4 skin changes in the first full growing season—following the first winter's dormancy—and 3 or 4 sheddings during the second. This would make a total of 7 or 8 exuviations (including the shedding at birth) when the snake has attained its second birthday. These skin-changing schedules, be it noted, were determined from average conditions among wild rattlers. They indicate a frequency definitely higher than that obtaining among adults.

Heyrend and Call (1951, p. 29), in their observations of a den of Great Basin rattlers (*C. v. lutosus*) near Salt Lake City, Utah, where the season of activity is much shorter than at San Diego, found that most of the juveniles entered their first hibernation with a single rattle, the button, although a few had acquired a second. They usually entered their second hibernation with 3 rattles, but some had 4. Few added more than a rattle per year after that. This is a slower shedding schedule than that noted among the *C. v. viridis* at Platteville, Colorado, where the modal string at the second hibernation was 5.

Fitch (1949a, p. 527), in his studies of the northern Pacific rattler (*C. v. oreganus*) in Madera County, California, found the modal string for snakes entering their second hibernation to comprise 4 rattles, and that those entering their third hibernation had 6 or even 7. Since most entered their first hibernation with a button, the average snake shed 3 times in its first full active season of about 7 months, and twice in the second. Fitch found (p. 533) that young rattlers, if stunted in growth, shed less frequently than the more normal juveniles.

From all of these data, we are justified in concluding that juvenile and adolescent rattlers in the wild shed from 2 to 4 times in their first full growing season, and

from 1 to 4 times in their second, and that the number of sheddings depends on the duration of the season of activity.

Some records derived from young captive snakes have been as follows: Of 5 captive red diamonds, 4 changed their skins 5 times in the first year, and one changed 6 times; in their second year, one changed 4 times and the others 3 times. A Colorado Desert sidewinder (*C. c. laterorepens*) exuviated 4 times in its first 7 months. Of 4 *scutulatus* × *unicolor* hybrids, 3 shed 6 times in their first year, and the other 5 times. A young *unicolor* shed 5 times in its natal year. In these cases there was, of course, no hibernation.

The most remarkable records of frequent skin changes in young captive rattlesnakes that I have seen were exhibited by 9 western diamonds (*C. atrox*) born at the Brookfield Zoo, near Chicago, under the care of the late Mrs. Grace Olive Wiley. I saw them at the age of 27 months, at which time the sheddings could still be ascertained from the complete or almost complete rattle strings of 5 of the 9. Including the birth change, one had shed 15 times, three 16 times, and one 17. On the average, they had shed every 52 days, or 7 times per year. The shapes of the rattle strings were different from the usual form in the wild, for the strings were smaller and more gradually tapering. What conditions of temperature, humidity, or food caused these abnormally frequent skin changes, I am unable to state, but at least these specimens indicate the degree to which rattlers can be affected by captivity, especially when there is no period of winter rest.

For a long time it was believed that rattlesnakes shed but once a year (Lawson, 1709, p. 129; Dudley, 1723, p. 295; Brickell, 1737, p. 147; Griffith and Pidgeon, 1831, p. 310). No doubt this belief was correlated with the imperishable, and even older, rattle-a-year theory. As late as 1876, Moran (p. 84) wrote to the editor of a sportsman's journal and told him that he had seen a timber rattler shed twice in a summer. The editor replied that it was believed that they shed only once annually, just before entering hibernation. Gradually the estimates of the rapidity of shedding have increased, culminating in Davenport's estimate (1943, p. 18) of once every 20 days during the active season, which is certainly much too short an interval, even for snakes in captivity.

It is impossible to judge the shedding intervals of wild adult rattlesnakes by the rattles of den aggregations, as has been done with juveniles and adolescents, since their strings are too seldom complete to afford peaks in numbers at hibernating time. For this reason dependence for adult data must be placed on the studies involving the marking and liberating of snakes, or on records derived from rattlers in captivity.

Fitch (1949a, p. 527), from his studies of *C. v. oreganus* in the wild, concluded that fully adult males shed about 1.5 times per year on the average, and adult females 1.1 times. Heyrend and Call (1951, p. 32) voiced the opinion that *C. v. lutosus*, under conditions of the shorter active season near Salt Lake City, rarely shed more than once a year when fully adult.

As to the shedding frequency of captive rattlers, the statistics in table 6:5, wherein each line represents an individual snake, were compiled from studies of adults at the San Diego Zoo. Each snake was at least 2 years old at the beginning of the compilation.

It will be seen that the sheddings per year vary from a low of one, in two Colorado Desert sidewinders (*C. c. laterorepens*) and one southern Pacific rattler (*C. v. helleri*), to a high of 3.9 in a Mexican west-coast rattler (*C. b. basiliscus*) and a timber rattler (*C. h. horridus*). The average for 297 years in the adult lives of 32

TABLE 6:5  
SCHEDULE OF SKIN SHEDDINGS

Subspecies	Years of observation	Sheddings	Average sheddings per year
<i>C. unicolor</i> .....	12	21	1.7
<i>C. unicolor</i> .....	6	13	2.2
<i>C. unicolor</i> .....	5	10	2.0
<i>C. b. basiliscus</i> .....	8	31	3.9
<i>C. b. basiliscus</i> .....	8	24	3.0
<i>C. adamanteus</i> .....	9	19	2.1
<i>C. atrox</i> .....	15	40	2.7
<i>C. atrox</i> .....	14	37	2.6
<i>C. atrox</i> .....	11	21	1.9
<i>C. atrox</i> .....	10	20	2.0
<i>C. tortugensis</i> .....	14	35	2.5
<i>C. r. ruber</i> .....	11	22	2.0
<i>C. r. ruber</i> .....	9	31	3.4
<i>C. r. ruber</i> .....	9	27	3.0
<i>C. r. ruber</i> .....	8	20	2.5
<i>C. r. ruber</i> .....	8	15	1.9
<i>C. r. ruber</i> .....	8	15	1.9
<i>C. r. ruber</i> .....	5	10	2.0
<i>C. v. viridis</i> .....	14	22	1.6
<i>C. v. viridis</i> .....	9	15	1.7
<i>C. v. lutosus</i> .....	6	18	3.0
<i>C. v. helleri</i> .....	15	38	2.5
<i>C. v. helleri</i> .....	7	19	2.7
<i>C. v. helleri</i> .....	7	7	1.0
<i>C. m. pyrrhus</i> .....	13	15	1.2
<i>C. h. horridus</i> .....	15	23	1.5
<i>C. h. horridus</i> .....	11	43	3.9
<i>C. h. horridus</i> .....	6	15	2.5
<i>C. h. atricaudatus</i> .....	6	23	3.8
<i>C. c. laterorepens</i> .....	6	9	1.5
<i>C. c. laterorepens</i> .....	6	6	1.0
<i>C. c. laterorepens</i> .....	6	6	1.0
Total.....	297	670	2.3

rattlers was 2.3 sheddings per year. The maximum, for any snake in any one year, was 6 in the case of a *basiliscus* (known to be 5 years old at the time); and the minimum none, in the case of one *horridus*, although it resumed shedding in the following year. One *atrox* showed remarkable uniformity, in that it shed twice a year every year for 10 years. Each of two *laterorepens* shed at annual intervals for 6 successive years. Notwithstanding that the snakes comprised in this record were at least 2 years old at the time they were first included, the statistics show a definite tendency toward a gradual decline in the frequency of shedding with age.

However, the two *basiliscus* each shed 4 times in their tenth year, and 3 per year in snakes at least 8 years old is not unusual.

As to the conditions under which these records were made, the adult snakes were offered food at biweekly intervals all year round. If an individual seemed too fat, the interval might be lengthened to 3 weeks. The temperature was maintained at 80° F. in winter; it may have run somewhat higher at times in summer, as no artificial cooling was provided and there was a considerable area of glass skylights. Loewen (1947, p. 53) tells of a massasauga (*S. catenatus*) that lived in captivity for a few days short of 14 years, during which it shed 26 times, or 1.9 per year. It shed 3 times in each of the last 3 years, which was more than in any of the early years.

From all of these data I should judge that adult rattlesnakes in the wild shed from about 3 times per annum where the climate permits activity almost all year, down to once per year where activity is limited to about 6 months of the year or slightly less.

Various conditions of health and diet have been stated to affect the normal shedding of rattlers and other snakes. Fraser (1936-37, p. 77) believed that well-fed snakes shed oftener than those that are fasting. Although this was doubted by Stabler (1939, p. 229), it is undoubtedly true of young snakes. Allen and Neill (1950a, p. 10) also found that rattlers shed less often if feeding poorly.

Allen and Swindell (1948, p. 7) reported that water moccasins shed more frequently when ill or when afflicted with skin infections. Neill (1949, p. 115) also concluded that injury accelerated shedding in snakes, although this is doubted by Perkins (1950, p. 35). Loomis (1951, p. 83) believed that a chigger infestation speeded skin changing in prairie rattlers (*C. v. viridis*).

Schaefer (1933, p. 1363) found shedding intervals to be affected by thyroid activity; reduced activity increased the frequency of shedding.

Additional discussions of shedding schedules will be found in Quelch (1891, p. 8), Guthrie (1924, p. 417; 1929, p. 351), Stabler (1939, p. 227), Falck (1940, p. 135), Fitch and Glading (1947, p. 116), and Stickel (1952, p. 9).

## LOCOMOTION

Since man saw his first snake he has pondered the puzzle of its motion. To see it flowing over the ground with effortless grace gives no indication that the propelling force is coming from within the creature itself.

"There are three things which are too wonderful for me, yea, four which I know not: The way of an eagle in the air; the way of a serpent upon a rock; the way of a ship in the midst of the sea; and the way of a man with a maid." Proverbs xxx: 18-19.<sup>17</sup>

According to Chateaubriand (1856, p. 112) the snake has "neither fins, nor feet, nor wings; and yet he flits like a shadow, he vanishes as if by magic, he reappears and is gone again, like a light azure vapor, or the gleams of a sabre in the dark."

John Ruskin (1869, p. 83) wrote: "That rivulent of smooth silver—how does it

<sup>17</sup> Anon. (1883a, p. 199) says the Hebraic wording leaves no doubt it was the serpent's method of progression that was deemed beyond understanding.

flow, think you? . . . Watch it, when it moves slowly:—A wave, but without wind! a current, but with no fall! all the body moving at the same instant, yet some of it to one side, some to another, or some forward, and the rest of the coil backwards; but all with the same calm will and equal way—no contraction, no extension; one soundless, causeless, march of sequent rings, and spectral procession of spotted dust, with dissolution in its fangs, dislocation in its coils.”

The puzzle of the snake’s motion lies in the lack of any apparent force exerted on the ground, such as is seen when an ordinary creature moves its alternating legs; there is no evidence of its pushing itself forward. Here is an attenuated body disposed in waves; and, seemingly without effort on its own part, it flows forward into new waves, as water might run down a slope within the banks of a stream. If the eye be focused on a single point of ground along which a brightly colored snake is passing, one will see the spots or rings glide by, along an unchanging, narrow path. The body decreases and is gone, yet all the while it seems to have exerted no push to cause the movement.

During the past few years there have been renewed attempts to explain the motion of the snake, seeking to show how the muscular source of the effort is converted into the even flow of the entire body. Among those who have advanced our knowledge of the mechanical principles involved, have been Fokker, Wiedemann, Mosauer, Gray, Lissmann, and Bogert, to whose works detailed references will later be made.

Although one method of crawling is both more common and less readily explicable than the rest, snakes actually employ four different kinds of propulsion to which the following names have been applied: Horizontal undulatory, rectilinear, sidewinding, and concertina. Rattlesnakes use all of these at times, although only one species (*C. cerastes*) is adept at sidewinding; and the concertina method is of relatively restricted utility. I shall now describe each of these methods, the mechanical principles involved, and the circumstances under which they are likely to be used. Although the four methods are sharply distinguished when practiced in a typical manner, they can be employed in such a way as to change, by degrees, from one to the other; and, indeed, a snake can simultaneously use one method anteriorly, while another is employed toward the tail.

Rattlers do not differ essentially from other snakes in their ways of crawling; their choice of method is dictated by their objectives and the character of the ground. But, as they are relatively heavy-bodied, they use rectilinear progression more frequently than do slimmer snakes, many of which, indeed, are quite incapable of moving in this way. Naturally, using rectilinear progression more, they use the commonest of the four methods—horizontal undulatory—somewhat less than do most other kinds of snakes, although they are quite capable of employing it when occasion requires. Also, one of the rattlesnakes, the desert horned rattlesnake or sidewinder, is, as its popular name implies, particularly adept at the method of crawling known as sidewinding, a distinction shared by only a few other desert snakes the world around.

#### HORIZONTAL UNDULATORY PROGRESSION

Most snakes normally crawl by means of the horizontal undulatory method—or, as it is sometimes called, the serpentine or sinusoidal. Yet, while the commonest

of the four recognized methods, it is, at once, both the most difficult to describe and to understand, as a simple problem in mechanics.

The snake, with its body in a series of side waves (fig. 6:5), glides smoothly along, each part of the body unerringly following the wavy path first taken by the head and neck. The waves are as nearly horizontal as may be permitted by the unevenness of the ground over which the snake is crawling and upon which the waves rest; it never uses one or more vertical loops such as that affected by an inchworm, which was the snake motion most commonly depicted in the prints in the old natural histories. This supposed method of progression by vertical loops has been attributed to snakes—including rattlers—even by fairly recent writers (Goldsmith, 1774, vol. 7, p. 183; Griffith and Pidgeon, 1831, p. 287; Martin, 1851, p. 197;



Fig. 6:5. Southern Pacific rattlesnake (*C. v. helleri*) in crawling position when using horizontal undulatory method of progression at slow pace.

Owen, 1866, p. 260; Roget, 1870, vol. 1, p. 361; Rivers, 1874, p. 509; Reid, 1889, p. 226) although denied by Aristotle many centuries before (Forster, 1937, p. 513).

The puzzle in the horizontal undulatory method of crawling is the conversion of the body waves—the lashing of the body from side to side—into longitudinal motion. One might expect that this lashing, if effective at all, would cause the entire body to slide across the ground, leaving a track as wide as the maximum width of the waves. Indeed, on a very smooth surface, this result is produced, for the lashing is highly ineffective;<sup>18</sup> and the same result may be noted in a swimming snake where the lashing produces a relatively slow forward motion in snakes unaccustomed to water. But give a snake a firm and rough substratum upon which to travel, and the lashing becomes converted into longitudinal motion, so that it ceases to be evident as lashing at all. The motion is not longitudinal in the direction of the objective, but along the body of the snake, as a file of ants might follow a winding path. Actually, the snake pushes backward against any irregularities in the ground that will prevent back-slippage, but the push is evident only if the objects pushed against are movable, as is the case when a snake traverses sand; and the mechanical principles involved in converting this backward push into the smoothly gliding body, following a narrow, wavy track, are by no means simple.

That a snake deliberately feels for, or seeks, irregularities in the ground that will serve as stationary pivots or anchors against which it can push, is shown by its

<sup>18</sup> De Lys (1948, p. 70) stated that in certain ancient rituals snakes were placed on smooth surfaces so they could not escape.

every action. Placed on the ground among an irregular arrangement of stones or the stems of bushes, the snake will dispose its curves in what seems to be a haphazard and irregular arrangement; but actually the curves are really so aligned as to take advantage of the nearest available pivots. But if the surface of the ground is more even, yet still has a high enough coefficient of friction to afford something against which the snake can push, then the curves followed by the snake are more regular. Coarse sand, uniform pebbles, or short stiff grass, comprise such surfaces. In these cases no particular irregularities stand out, and the snake will usually take the form of two successive sinusoidal curves, one on each side of a central axis that points toward the objective. But the number and depth of the curves depend on the character of the surface, the habitus of the snake (including the length of its tail), and the urgency of its movement, so that, in practice, two equal and complementary waves are seldom seen. A prowling snake will employ more and shallower curves than one that is frightened and seeking speedily to escape.

Various authors (e.g., Mosauer, 1932c, p. 583) have shown that a snake's vertebral column, although resistant to stretching or compression along the axis, is capable of lateral flexure with little resistance, and so is well designed to transmit propulsive forces along the body from one element to the next, as a locomotive in the center of a train on a wavy track would have no difficulty in transmitting a uniform motion to every car in a train, whether ahead or behind.

Despite statements to the contrary, those who have studied the mechanical principles of sinusoidal snake locomotion (e.g., Mosauer, 1932c, p. 585) are agreed that the ventral plates are not used ratchetwise as a part of the mechanism of horizontal undulatory motion, nor is there rib-walking, as is sometimes stated.

Continuing the analogy of the train on the wavy track, we may note that the movement of the train does not depend on the presence of a propulsive force in every car. Furthermore, one particular car need not always be the locomotive. Judging by the pushed-up piles of sand that are left by a snake moving on the surface of fine sand or dust, we know that the greatest lateral pressure is exerted at the outer, rear section of each loop (Mosauer, 1935b, fig. 6; Cowles, 1941, plate 4, fig. 1; Grinnell and Storer, 1924, plate 40, fig. b). It is as if each car of a train on a wavy track should become a locomotive just as it swings outward toward the extreme bulge of the curve, only to lose its power to propel, thus becoming an inert follower, when this outer bulge is reached. This point of maximum application of lateral pressure is evident, not only from the sand piles that border snake tracks, but can be observed by means of watching a snake moving through short grass, or, as is done by some experimenters, from the motions of sticks or bristles suspended from above a moving snake (Mosauer, 1932b, p. 201).<sup>19</sup>

It remains to be shown how the lateral pressure against a pivot or anchorage point can be exerted by the snake's musculature in such a way as to convert the pressure into longitudinal forward motion along the body of the snake. Of this mechanical problem, solutions have been proposed by Fokker (1927, p. 65), Mosauer (1932b, p. 199; 1932c, p. 583), Gray (1946, p. 101), and Gray and Lissmann

<sup>19</sup> These tests also showed that snakes, when crawling by this method, were not dependent on their ratchet-like ventral plates, although it is true that on soft, yielding media, the sharp ventrolateral ridge along the ventrals of some sand-dwelling snakes, such as that found on the shovel-nosed snake (*Chionactis occipitalis*), does aid progression (Mosauer, 1934, p. 58).

(1950, p. 354). Fokker's English summary (p. 71) is as follows: "The locomotion of serpents is explained, after an analysis of a mechanical analogy, by assuming muscular action which tends to stretch [straighten?] the body where the curvature of the path decreases, and which tends to bend the body where the curvature of the path increases in the direction of motion."

Mosauer shows, by a parallelogram of forces, how a lateral pressure against an obstruction can be converted into a longitudinal motion. The snake presses the posterior part of a body wave against a stationary object, the reaction of which is perpendicular to the snake's body at the point of contact. The resultant force and motion are directed longitudinally along the center line of the snake's body. As each successive element of the body passes the pivot point, it, in turn, is pressed against that point and becomes the motive force pushing the body forward. It is as if our train of cars, instead of being activated by forces applied to the wheels, were mounted on a flexible track that permitted one of the cars on the rearward half of a side wave, to push against a telephone pole close to the track, at the same time sliding along the track. The train would be caused to advance along the track, with each successive car pushing against the pole as it passes.

Mosauer made a close study of snake musculature and correlated his theory with the body flexure that must be derived from the muscles, it being remembered that muscles can exert force only by shortening, that is, by tension.

The weakness in Mosauer's exposition lies in his failure to show simultaneous parallelograms of forces for several pivot points, without which it is not demonstrated how the snake can exert pressure on any one.

This deficiency has been supplied by Gray (1946, p. 102), who, by means of a mechanical analogy involving sections of hinged rods and springs to represent the snake's skeleton and muscles, reached the conclusion that the motion is not only dependent on adequate pivots, or points of resistance, but that the shape of the curves is of paramount importance, it being necessary that "the angle which the axis of any segment makes with that of the segment immediately in front of it must be greater than that which it makes with that of the segment immediately posterior to itself" (p. 105). Gray summarizes his theory of serpentine (horizontal undulatory) motion as depending on the following three factors: "(1) The body must be thrown into one or more curves each of which exhibits an increase of curvature when measured toward the head of the animal. (2) Active muscular tension must develop in the axial muscles which lie on the same side of the body as that in which the curve is increasing. (3) The body must be subjected to at least three external resistances acting normally to the surface of the body. The propulsive force is the resultant of the reactions exercised by all these external resistances" (p. 119).

Gray and Lissmann (1950, p. 354) made studies of sinusoidal motion using a European grass snake operating in a channel with zigzag walls, against pendulums, or against rigid pegs. They determined the intensity and direction of the muscular effort exerted by the snake, and the sliding friction of the surface crawled over, which friction the snake must overcome. They concluded that "the forward movement is due to the operation of the vertebral column as a series of levers" (p. 367).

As one watches a rattlesnake crawl, using the undulatory method, it is apparent that it seldom has cause to adopt a series of even, balanced curves, for this is done

only where the ground surface is without irregularities, as, for example, on smooth sand or the surface of a lawn. Under other more usual conditions, the body takes advantage of whatever irregularities that may serve as pivots against which to push, such pivots being on both sides of the line or axis that represents the direction of travel. The head and neck are raised slightly; they face forward, and deviate less from the axis of travel than do the waves of the body that follow. Thus it is evident that the pivots are not discovered by sight, but by the pressure of the body against them; and what is most amazing is the way in which, when a forward element of the body has—if I may use anthropomorphic terms—discovered and used a suitable obstruction against which it may push, each succeeding body element follows in exactly the same path, so that each in turn pushes against the obstruction when it arrives there. And, of course, there are always several such pivots being pushed against simultaneously as the snake glides along.

When a snake is advancing by undulatory motion in a soft medium such as dust or fine sand, it makes its own pivots in the form of raised sand crescents on opposite sides of the axis of travel. The posterior points of the crescents are always nearer the central axis than the anterior; in fact, they overlap the axis. The crescents become longer and higher as the snake moves, so that they are more useful to the posterior part of the snake's body than to the anterior.

That additional studies of horizontal undulatory motion are desirable goes without saying. The shapes of the curves made on uniform surfaces should be plotted and analyzed, and then correlated with such variables as relative speed, substratum texture, ground slope, body shape (slim compared with heavy-bodied snakes), and tail length. Such studies can be made only on uniform substrata. Although the fundamental kinematics of sinusoidal movement are now understood, much still remains to be done on this problem that puzzled the proverb-maker Agur so long ago.

#### RECTILINEAR PROGRESSION

Rectilinear progression is a method especially useful to large thick-bodied snakes, such as pythons, boas, and the larger vipers. Rattlesnakes of all kinds, particularly adults, employ it extensively, chiefly when they are prowling and unhurried. It is one of the two methods of crawling—the other is the concertina type—in which the ventral scutes play the important part formerly attributed to them as essential to all types of locomotion. This method has been called the "snail motion" by Wiedemann (1932, p. 572) and the "caterpillar" by Mosauer (1932b, p. 207; 1932c, p. 583), but Gray's designation "rectilinear" is to be preferred.

The motion has long been recognized, since anyone who has watched some of the boas or pythons move must have observed it. The method of operation was first described in detail by Home (1812, p. 163), and has since been elaborated by Wiedemann (1932, p. 572), Mosauer (1932b, p. 207; 1932c, p. 585), Bogert (1947b, p. 253), and Lissmann (1950, p. 368).

Most descriptions of snake motion, whether undulatory or rectilinear, since Home's paper of 1812, have pictured the snake as "walking on its ribs"; indeed the idea dates back at least to Tyson in 1683 (p. 28). But while gradually it came to be recognized that rib movement did not play an essential role in the undulatory method, the rib theory has persisted in the explanation of rectilinear motion, even

to the present time (Gray, 1946, p. 101). However, as Mosauer, Bogert, and Lissmann have pointed out, even in this method of propulsion, the ribs are not employed in the sense of "rib-walking," for the tips of the ribs remain unmoved relative to the vertebral column. On the contrary, the crawling is effected by reciprocating movements between the snake's skin and its body. As Bogert has indicated, it is possible only to snakes having a loose attachment between the skin and the interior undersurface of the body itself, a condition absent in many kinds of snakes.

In operation, a section of the skin of the belly is drawn forward so that the ventral scutes in that section appear to be bunched. This part of the body is then pressed on the ground so that the sharp rear edges of the ventrals may engage any available imperfections of the ground surface and thus be prevented from slipping back. Then the body slides forward within the skin, pulled by appropriate muscles, until it once more is in normal alignment with the skin. Then once again the skin slides forward and the process is repeated. During the forward motion, the skin is raised so as to clear the ground, or at least enough to reduce the friction of its advance. When it comes to rest, it is pressed into the ground to secure an anchorage against slipping back, while the body is being pulled forward. Thus we have, in effect, a ratchet in which the ventral scutes are the teeth, engaging such ground irregularities as they may hook on. Above this ratchet we have a muscle-operated reciprocation between the skin and body. It should be made clear that the reciprocating movements are only between the lower surface of the body and the adjacent skin, for there is no similar motion dorsally; in other words, the body and skin do not have relative motion in their entirety but only between their lower surfaces.

Furthermore, the ventral surface of the skin is not all acting in the same way at the same time, for some sections are pushing backward against the ground, while others are raised and disengaged from the substratum. For what has just been described is the occurrence at a single segment of the body; it remains to mention the correlation between segments composed of groups of ventral scutes. As one watches an individual segment, he will clearly see the skin of the ventrum raised and advanced—relative to the stationary skin of the dorsum—then lowered and pushed back. This involves a compression of ventrals at one point and a corresponding spreading at another. If the body is viewed as a whole, it will be seen that these compression waves pass backward from the head toward the tail. They are always accentuated or more intense at mid-body, where the weight of the snake makes the ratchet action most effective; they are little in evidence at the neck and again diminish in intensity at the tail. Generally, as a snake is moving uniformly, several of these compression waves—with suitable interspaces—will be observed following each other tailward. These movements can be visualized in the excellent diagrams of Lissmann, 1950.

These successive and uniformly spaced waves down the length of the body are not always in evidence. Sometimes it will appear that the snake is using only one or more short sections of the body for the reciprocating motion, as if these parts were supplied with legs and the rest were not, and all the motion were generated in them. This is particularly evident when only a short section—usually somewhat anterior to mid-body—is being reciprocated. In such a case one may see a single

group of ventrals slide forward, grip the soil and remain stationary while the body is pulled up to them.

It might be thought, from the description of rectilinear progression and the term itself, that it is suitable only for proceeding in a straight line. Such is not the fact; a snake can turn a sharp corner, or even reverse its direction, without deviating from the rectilinear method.

Rectilinear progression is often used in conjunction with other types. When combined with the undulatory, it partakes of the nature of concertina motion. These combinations are usually employed on smooth or difficult surfaces, or where the snake is confined to a narrow channel. A rattlesnake proceeding down a slight incline was observed to start with an undulatory movement, after which it coasted down the slope by rectilinear progression.

The rectilinear type of progression is probably the normal method used by adult rattlesnakes when they are prowling about, and have not been startled. Since a straight track is left, it is easy to tell when a snake has been using rectilinear locomotion, but it is sometimes impossible to tell in which direction it has gone, as no tell-tale piles of pushed-back earth or sand are left, such as mark the path of an undulating snake. However, if there are small depressions in the path of a crawling snake, sand or earth will be dragged forward into them; these will be present in the part of the depression opposite to the direction in which the snake has crawled. In many areas in the United States, rattlers are the only snakes using the rectilinear system and therefore their tracks may be easily identified.

A few field observations of rectilinear motion by rattlesnakes are those of Rutledge (1932, p. 53; 1935, p. 524) and Ditmars (1936, p. 358) on the eastern diamondback (*C. adamanteus*); Mosauer (1933, p. 15; 1935b, p. 21; 1936b, p. 15) on the western diamond (*C. atrox*) and the red diamond (*C. r. ruber*); and Cowles (1945b, p. 221) on the Colorado Desert sidewinder (*C. c. laterorepens*). Charles H. Lowe, Jr., has written me of seeing straight sidewinder tracks; and Charles M. Bogert has mentioned finding rectilinear tracks of the western diamond (*C. atrox*) and the prairie rattlesnake (*C. v. viridis*). Among captive snakes, C. B. Perkins has noted it to be the common method of progression of every species of rattlesnake that has been exhibited at the San Diego Zoo, as they crawl leisurely about their cages.

Mosauer (1933, p. 16; 1935b, p. 21) calls attention to the fact that rectilinear motion is particularly useful where there are many obstructions, for these interfere more with an undulating or sidewinding snake than one progressing in a straight line. He mentions a western diamond (*C. atrox*) that followed an almost straight course in visiting every shrub or bush-covered hillock in its path, 34 in all, in a single night's prowl, and made only a few undulations on the entire trip. He noted, however, that while this snake used the rectilinear method on the level or going down a slope, it reverted to horizontal undulatory or concertina types of crawling when going uphill. Bogert (1947b, p. 253) believes the sidewinder to be a notable exception among the rattlesnakes in not using rectilinear progression for prowling. Sidewinder tracks show that it ordinarily adopts sidewinding when cruising about at night.

The straight trail of a snake using rectilinear progression has sometimes led to the assumption that the snake was moving by means of vertical undulations

(e.g., Rivers, 1874, p. 509). It is true that vertical undulations are involved, but only to the very slight extent that the forward moving ventral scutes are made to clear the ground, as they are pushed forward. They make no high vertical loops such as were pictured in so many of the early illustrations of moving snakes.

#### SIDEWINDING

Sidewinding is the natural way of crawling of several kinds of desert snakes, a method followed whether they are hurried or merely prowling. It is also used by other snakes when under the necessity of negotiating smooth surfaces on which their usual means of progression are found to be ineffectual. By no means all ophidian dwellers on shifting desert sands are sidewinders—meaning by this term a snake that customarily uses sidewinding progression—for most snakes in such circumstances, including various species of rattlers, still adopt horizontal undulatory or rectilinear motion, and use them with a satisfactory efficiency. Also, it should be pointed out that when a snake, not normally a sidewinder, attempts to crawl in this manner as a temporary expedient, it is usually a rather amateurish effort with neither the grace nor efficiency of the professional. Those who have seen only the thrashing of an alarmed snake on a smooth surface—although it does result in sidewinding of a kind—have little conception of the smoothly flowing grace and rapid transverse movement produced by the deep lateral curves of the true sidewinder.

The perfect exponents of sidewinding motion in the Old World include the two Saharan vipers, *Aspis*<sup>20</sup> *cerastes*, the horned viper, and *A. vipera*, the common sand viper, and also *Echis carinatus*, the saw-scaled viper. Their peculiarities of motion have long been known. Lucan, the Roman poet of the first century A.D., mentions the horned viper as moving with a twisting backbone (Riley, 1909, p. 368), and another translation describes it as wandering whichever way its spine makes it turn (Duff, 1928, p. 559). Thus the strangeness of its movements was attributed to a defect in the spine—in fact, according to legend, a broken back resulting from a chance trampling by Helen as she was eloping with Paris (Nicander, ed. 1953, p. 49; Pliny, 1855–57, vol. 2, p. 285, f.n. 76; Topsell, 1608, p. 198). Pausanias, writing about A.D. 150 (Jones translation, 1918–35, vol. 3, p. 363) refers to the horned viper as moving with a sidelong motion as do crabs, an apt simile. Corkill (1932a, p. 609) says that in Iraq this snake's peculiar habit of "coiling to a flank" has given it the same vernacular name as the freshwater crab. According to Doughty (1888, vol. 1, p. 314) the Arabs refer to this snake as the one "that moves on her side." Another term for sidewinding is that of the Maricopa Indians, who call our sidewinding rattlesnake the "left-handed snake."

Lacépède (1788–89, vol. 2, p. 78; Kerr, vol. 3, p. 268) says that the Saharan horned viper "never advances straight forwards, but always in curves, and winding from side to side"—almost an anticipation of the American term "sidewinder." Bruce (1790, vol. 5, pp. 198–210) wrote a lengthy description of the horned viper, including the remark that it "moves with great rapidity, and in all directions, forward, backward, and sideways. When he inclines to surprise any one, who is too far from him, he creeps with his side toward the person, and his head averted,

<sup>20</sup> Until recently these snakes were placed in the genus *Cerastes*.

till judging his distance, he turns round, springs upon him, and fastens upon the part next to him." There is confusion here between progression and the striking coil, and sidewinding, for a time, came to be interpreted as a method of attack rather than mere locomotion; for Bruce's statement was reprinted or paraphrased in many subsequent natural histories (e.g., Shaw, 1802, vol. 2, p. 390; Griffith and Pidgeon, 1831, p. 371; Royal Natural History, 1896, vol. 5, p. 237), thus delaying for years an appreciation and understanding of this peculiar method of progression adopted by some desert snakes.

Another Old World sidewinder is the South African horned viper (*Bitis caudalis*) of the Kalahari Desert and adjacent areas (Rose, 1950, pp. 222, 307). The dwarf puff adder (*Bitis peringueyi*) is also a sidewinder (Mertens, 1953, p. 155), and *Bitis cornuta* may sidewind. The Iranian horned vipers of the genus *Pseudocerastes* are probably sidewinders.

Our own sidewinder, the small desert rattlesnake (*Crotalus cerastes*) with the alternative name of horned rattlesnake, attracted attention from the early days of the travelers who met it while crossing the southwestern deserts. They were quick to note its peculiar motion and to invent the appropriate term "sidewinder," which became current as early as 1875. The term is often misused in applying it to rattlesnakes of various species that sidewind only rarely and imperfectly, or to snakes that have the reputation of striking sidewise. But it is universally applied to the true sidewinder or horned rattlesnake; and now the term "sidewinding" has come into general use to describe the method of locomotion of this snake and its Old World desert analogues. The alternative term "crotaline" locomotion suggested by Gray (1946, p. 113) is not to be recommended, since most crotaline snakes do not sidewind as a normal means of progression; and the Saharan vipers, which are perfect exponents of the motion, do not belong to the family Crotalidae.

The sidewinding progression is difficult to describe. Hogner (1938, p. 110) says that it befuddles the observer. Holt (1939, p. 44) has described the motion from an inspection of motion pictures, but it would seem that his subjects were not throwing the loops as far out, laterally, as is normal. Motion pictures of a sidewinder at a natural gait, when slowed up on the screen, are quite effective in demonstrating the sequence and co-ordination of the motions.

The first investigator to make a really adequate analysis of the movements and forces involved in sidewinding was Mosauer, his more important papers being those of 1928, p. 201 (with Wallis); 1930, p. 179; 1932b, p. 205; and 1932c, p. 585. The description that follows is largely based on Mosauer's analysis, somewhat amended by my own field and laboratory observations.

Essentially, sidewinding involves a side-flowing or looping motion whereby only vertical forces (rather than transverse) are applied to the supporting surface. The track comprises a series of short, separated straight lines, set at an angle of about  $30^\circ$  with the direction of progression, each line approximating the length of the snake (fig. 6:6). If the track be in fine sand, and undisturbed by wind, the impressions of the ventral scutes can be clearly seen, for there is no transverse or sliding motion to obliterate them. Each section of the track has a fairly evident J-shaped mark (made by the head and neck) at one end, and a T-shaped terminus (made by the tail) at the other. The direction of progression, if one desires to track the snake,

is that toward which the hook of the J is pointing; however, the T-shaped mark left by the tail is nearer to the destination than the J made by the head.

To describe the motion of the sidewinder analytically, it is necessary to segregate several elements of motion that the snake executes simultaneously. Assume a snake outstretched on the ground, with the body lying at an angle of about  $30^\circ$  with the projected line of travel, but with the tail, rather than the head, pointing obliquely toward the objective (fig. 6:7). Using the central part of the body as an anchor, the head is projected forward in such a way that the anterior third of the snake makes an angle of about  $60^\circ$  with the rest of the body; in so doing the head and neck



Fig. 6:6. Track of an adult sidewinder traveling from left to right. The lower marks (rather less J-shaped than usual) were made by the head; the upper marks by the tail. The small tracks were made by beetles. (Photograph taken in the sand dunes at Sandy Beach, Salton Sea Wild Life Refuge, Imperial County, California, by Dr. Raymond B. Cowles.)

form an angle of  $30^\circ$  with the line of progression, but on the opposite side of that line from the angle made by the body. The head and neck in advancing do not touch the ground until they reach a new anchorage point, although they are raised so slightly that one must have the eye close to the ground to note the clearance. Now the head and an inch or so of neck are brought into contact with the ground and serve as a new anchor, and from this anchor the snake lays out its body forward toward the objective—not directly toward it, but at an angle of  $30^\circ$ . As the body is being laid out, with the tail toward the objective, there is a sharp crook at the neck so that the stationary head faces in the direction of progression, although the body is being advanced farther in that direction than the head itself. Then again the head reaches forward for a new anchorage and again the body is laid out in advance of it. But always in transferring from one anchorage to the next, whatever part of the body is in transition is raised slightly above the ground, so that the surface offers no resistance to this part of the movement, and no track is made: tracks are left only where the body is laid down obliquely in advance of the head. By this means virtually no transverse forces are applied to the supporting medium: only vertical forces are exerted, and the track is not a sinuous line, but a series of separate short straight lines, arranged in echelon toward the destination. Each

section of track has a length equal to that of the snake; and, as only vertical forces are applied, with no sliding, the imprints of each ventral scale are to be seen in the sand.

Primarily, sidewinding represents the most efficient use of a loose supporting medium, such as sand, which can offer little resistance, and therefore little reaction, to transverse forces directed across the surface (as do the sticks, stones, and irregularities of ordinary firm ground by which the typical snake aids its sinuous

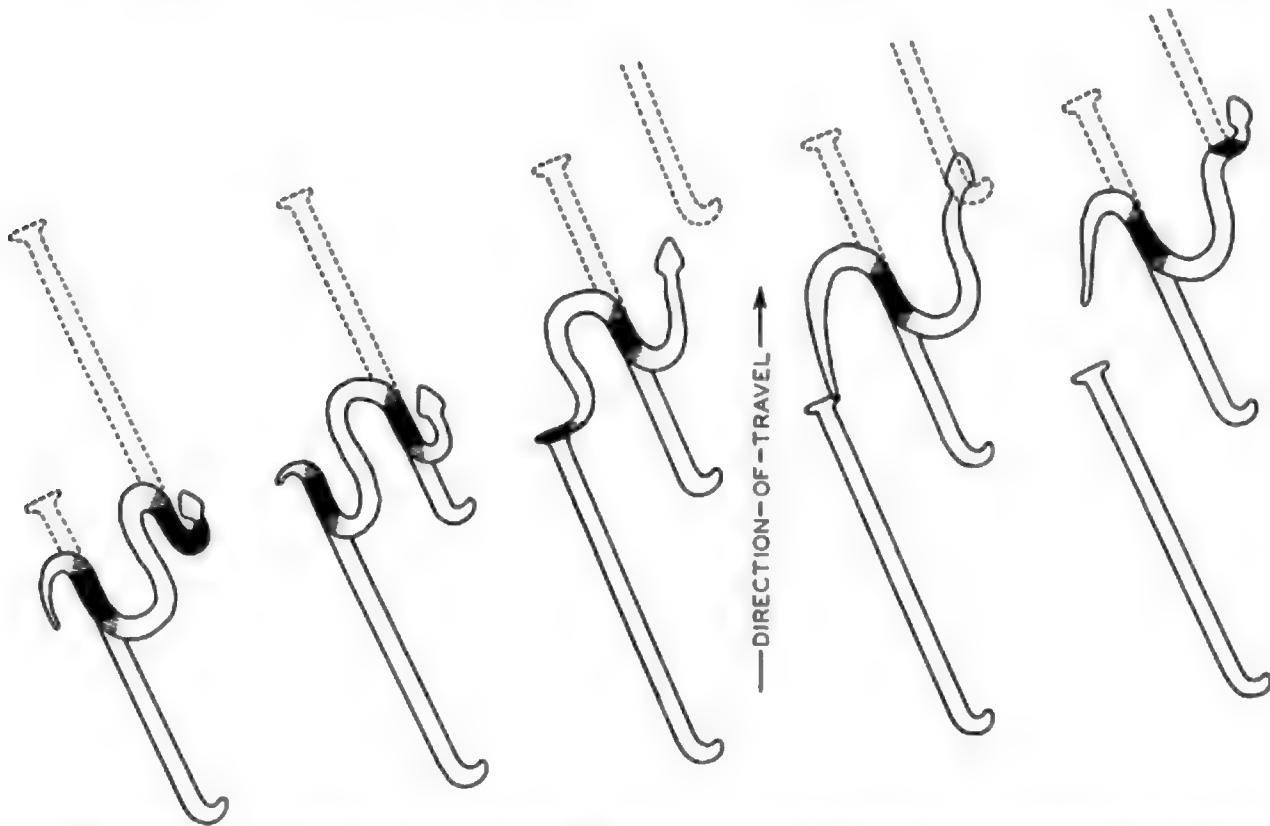


Fig. 6:7. How a sidewinder makes its tracks. Consecutive positions of a sidewinder's body in relation to the tracks. The solid track-outlines have already been made; the dotted outlines are yet to be made. Only the solid-black sections of the snake's body are in contact with the ground; the rest of the body is raised sufficiently to clear the ground. (After Mosauer, with modifications.)

progression), but can exert a considerable resistance to forces applied vertically. Just as a creature on foot can negotiate sand where a wheeled vehicle cannot, because the foot passenger advances the body while pressing successively on a series of temporary anchorages—the footsteps—so the sidewinder advances by using successive parts of its body as temporary supports from which other parts of the body are thrust forward.

A person watching a sidewinder will see no resemblance between the motion as I have described it—throwing out the head, laying down the body, throwing out the head again, etc.—and what the snake seems to be doing; for, as I have said, the snake telescopes these operations by executing several simultaneously. Long before the tail has been placed, at the end of the laying down sequence, the head has already reached out for a new anchorage, so that the moving snake is never, even for an instant, fully outstretched along any one of its tracks. As a matter of fact, it is always touching at least two tracks at once, with that portion of its body between tracks arched slightly to clear the ground surface; and at the time the head is first

touching its next anchorage, the tail-tip is just leaving the track two steps behind, so that for a moment in transition the snake may actually be in contact with three tracks at once.

From the standpoint of step-by-step analysis, this is an accurate statement of what the snake does, but from a pictorial standpoint, it could hardly be less informing. A sidewinding snake may best be described as one with a loose S-curve in its body; as the curves undulate the body appears to flow smoothly (and with a most unexpected rapidity) sideways across the sand. There is no hesitation, no pause in the even and continuous movement, such as might be inferred from the analytical description. Why the motion is said to be sideways is this: if a line be drawn from the snake's head to its tail and this be considered the snake's axis (although it is not outstretched, but in an S-curve), the line of progression will be seen to be perpendicular to this axis. In ordinary horizontal undulatory snake-motion, it will be remembered that the progression is in the direction of an imaginary axis from tail to head. But a sidewinder goes sideways as compared to the direction that a typical snake having the same S-curve would take—hence "sidewinding."

There are certain variations in sidewinder tracks that are probably caused by such conditions as temperature, speed, ground slope, and surface texture. It has been observed that the separation between successive tracks (measured perpendicularly) varies from 15 to 32 per cent of the length of the snake (exclusive of head and tail), the parallel overlap between tracks ranges from 25 to well over 50 per cent of the length of the snake, and the angle between the tracks and the line toward the objective varies between  $15^{\circ}$  and  $35^{\circ}$ . The more acute this angle, the narrower is the relative separation between successive tracks.

Sidewinding does not necessarily involve the use of the section of the neck immediately behind the head as the initial anchor for a succeeding stretch of track. The head can be kept well elevated, either for defensive or observational purposes, and the rest of the body can carry out the sidewinding method quite effectively. This is customary when a snake is moving away while threatening an intruder. Although some people believe that sidewinders can only sidewind to the right or to the left, actually they are equally adept in both directions.

Sidewinding is not only a solution of the problem involved in an unstable substratum, but is efficient from the standpoint of both speed and distance. Mosauer (1935a, p. 7; 1935b, p. 24) made 41 trials with 7 sidewinders (*Crotalus cerastes*) in their native habitats. He reached the conclusion that they were capable of speeds of 0.8 to 0.9 meter per second (1.8 to 2.0 miles per hour). He thought they might reach 3 miles per hour in sudden lunges for short distances. This is about half the speed of the fastest snake with which Mosauer experimented, the red racer, *Masticophis flagellum piceus*, a quite remarkable result, as rattlesnakes are slow and sluggish compared with racers. He concluded that sidewinders prowled at a speed of about 0.3 mile per hour. He thought (1933, p. 16; 1935b, p. 24) that they might wander as far as 1,000 feet in a single night; in fact, he found one hardly exceeding 10 inches in length that seemed to have gone that far. He traced another through the sand dunes west of Yuma for 2,834 feet, but concluded that this might have represented a two-night ramble. He found sidewinders erratic in their wanderings, seldom moving in a uniform direction, but taking zig-zag or circular courses, as one might expect of an animal on the prowl for prey. They were inclined to avoid

hills and bushes. Charles H. Lowe, Jr., tracking sidewinders in the vicinity of San Felipe, Baja California, also found their wanderings to be rather haphazard, without continuity of direction.

Many kinds of snakes that normally use other means of progression will sidewind under particular circumstances, especially if frightened while on smooth surfaces. Some sidewind with considerable success, the garter snakes, *Thamnophis*, for example; whereas others achieve but little more motion than would be secured by purposeless thrashing. Cowles (1941, pp. 133, 139) has shown that heat or fright will stimulate sidewinding by little desert snakes such as the shovel-nose (*Chionactis occipitalis*), the leaf-nose (*Phyllorhynchus decurtatus*), and the spotted night snake (*Hypsiglena torquata deserticola*). But they do not raise the body clear of the ground between the separate tracks, as does the true sidewinder, and the motion is relatively inefficient. Sidewinding in these snakes seems to result from an attempt to gain traction by pressing a part of the body to the ground while moving another. The body loops are not so wide laterally as those of the true sidewinder, and the movements are not well co-ordinated.

I have experimented with a number of subspecies of rattlesnakes, including *atrox*, *ruber*, *scutulatus*, *viridis*, *helleri*, and *pyrrhus*, on polished wood or linoleum floors to determine the degree to which they would adopt sidewinding on surfaces unsatisfactory for ordinary snake locomotion.<sup>21</sup> In general, although it was noted that all of these rattlers could and did sidewind, the motion was far from being a facsimile of the practiced grace of the sidewinder. First, the coils were not as widely thrown, and they were more nearly perpendicular to the axis of the body rather than at a sharp angle, as with the sidewinder. The several elements of motion were not even and continuously flowing; rather, they tended to be spasmodic and separate. The result was a much reduced efficiency, as measured by speed and expended effort. Some of the rattlers were virtually reduced to purposeless thrashing, or at least to a continuous effort to find irregularities in the floor surface that might serve as pegs against which to push the body. One southern Pacific rattler (*C. v. helleri*) was fairly successful; and Dr. R. B. Cowles has advised me by letter that one western diamond back (*C. atrox*), a snake that lives in sidewinder territory, but does not ordinarily sidewind, when placed on linoleum went into perfect sidewinding and flowed across the floor without the slightest effort or confusion. In my experiments, I found that much depended on the snake's objective and the degree of its alarm. Those that were not unduly frightened tried all forms of locomotion, at times simultaneously with different elements of the body; they mixed all combinations—undulatory, sidewinding, rectilinear, and concertina—in their endeavors to get a purchase on the smooth floor.

The fact that living in a sandy area does not automatically produce sidewinding is demonstrated by the snakes that occur along the edges of the sand dunes bordering the east side of the Salton Basin in Riverside and Imperial counties in southern California. Particularly common here are the shovel-nose (*Chionactis occipitalis annulata*), the leaf-nose (*Phyllorhynchus decurtatus perkinsi*), the sidewinder (*C. c. laterorepens*), and the western diamond rattler (*C. atrox*). By their tracks it is shown that when prowling at night the two first-named snakes use horizontal

<sup>21</sup> Incidentally, sidewinders traverse such surfaces quite as readily and rapidly as they would any surface to which they might normally be accustomed.

undulatory progression, whereas the western diamond, a much larger snake than the others, employs the rectilinear method. Only the sidewinder sidewinds. Similarly, in the Mojave Desert, the sidewinder is the only snake to adopt this way of crawling, for other, equally common snakes inhabiting the same terrain, including the glossy snake (*Arizona elegans candida*) and the Mojave rattlesnake (*Crotalus s. scutulatus*), are able to satisfy their needs with more orthodox methods of progression. It is interesting to note that although snakes that do not regularly indulge in sidewinding will approach this method when subjected to substratum conditions wherein it is superior to all others, sidewinders, on the contrary, do not abandon their usual mode of progression when on a hard, rough surface well suited to the undulatory or rectilinear methods. They are quite capable of using either, but seem to find their standard method equally serviceable on rough ground. It is only when crawling through the closely spaced stems of bushes that sidewinding must be abandoned. That they are not restricted to the sidewinding method has been demonstrated often in both field and laboratory. I have seen captive sidewinders use all the other motions for short distances—horizontal undulatory, concertina, and rectilinear. Charles H. Lowe, Jr., watched one in the field using the latter method; and Mosauer (1933, p. 15) noted that, on first emerging from ground holes in the evening, they used the concertina method for a short distance until they were warmed up. He also observed cases in which sidewinding was abandoned in favor of rectilinear motion for some distance (1935c, p. 33).

Why this particular rattlesnake should have become so adept at sidewinding must remain a matter of speculation. It is probably significant that their Old World analogues are of about the same size and body proportions. It is hardly necessary to point out that sidewinding was developed independently by these snakes in the Eastern and Western Hemisphere deserts. The sidewinder of our American deserts is more closely related to other rattlesnakes that do not sidewind, than it is to the sidewinding vipers of Asia and Africa. As a corollary it may be said that, although a sidewinder has been developed among rattlesnakes, the rest of the rattlers are no more adept at sidewinding in emergencies than snakes of other genera—*Thamnophis*, for example—that have not produced any sidewinding relatives.

Whatever conditions of sand surface, body contact surface, and bulk caused these particular snakes—and not other desert dwellers—to adopt sidewinding, the fact should not be lost sight of that it is so deeply ingrained as not to be abandoned when the snake lives on surfaces where sidewinding is not superior to the more customary means of progression. A young sidewinder that has never experienced sand sidewinds at birth.

Cowles (1953, p. 13) has pointed out that the complete adoption of sidewinding was a gradual development, just as was the change in ecological conditions that produced it. The sand dunes were a final accession. With increased aridity, plants became more widely separated and bare ground suitable for sidewinding more prevalent. The bushes affording adequate shade were scattered. With lethal surface temperatures, a type of locomotion entailing both speed and a minimum body contact with the ground became advantageous, and sidewinding fulfilled these needs.

The similarity of the methods developed independently in the widely separated

Saharan and American deserts is quite surprising. Watching both the Saharan horned viper, *Aspis cerastes*, and our local sidewinder, *Crotalus cerastes*, at the San Diego Zoo, I observed that the motions seemed to be precisely similar. It is possible that the African snakes raise their heads a little higher in seeking the next anchorage, and that their bodies clear the sand a little less in the transfer between tracks.

#### CONCERTINA PROGRESSION

The concertina type of progression was first dignified with a separate name by Wiedemann (1932, p. 577), although the method had been mentioned before, as, for example, by Martin (1851?, p. 197), Owen (1866, p. 259), and Stradling (1882, p. 377). Wiedemann called it the "earthworm" type, but I prefer Gray's designation (1946, pp. 101, 110) of concertina movement; for, as Mosauer (1932b, p. 208) has pointed out, Wiedemann's name is misleading, in that the earthworm progresses through alternately lengthening and compressing portions of its body, a method impossible for snakes, although occasionally attributed to them.

In the concertina movement, the central part of the body is alternately gathered into two or more sinuous curves, and then restraightened. While the longitudinal distance occupied by the central part of the body is being shortened, by change from a straight to a wavy form, the snake anchors its head and neck, so that the shortening results in drawing the tail forward. Then the central curves are again straightened so that the longitudinal space occupied is again lengthened; but, as this is being done, the tail is anchored so that the head and neck are thrust forward. Hence, with each complete cycle of movements the entire snake advances by the difference between the lengths of the snake when in its straightened and waved positions.

The concertina method has been described in detail by Gray (1946, p. 110) and by Leutscher (1950, p. 392). Gray points out that the alternate anchoring effects of the head and tail sections are aided by the ventral scutes, which operate, in cooperation with the roughnesses of the ground, as little ratchets.

Actually, the concertina method is not the normal means of progression of any snake; rather, it is used under particular circumstances as, for example, when a slow, hesitating advance is desired. It may be employed by a snake investigating an object whose nature is obscure, in which case there may be considerable pauses between the alternations. I have seen it used by a king snake stalking a young rattler; and I believe it a particularly satisfactory method for stalking because it has two advantages over the more rapid undulatory method: First, the head is not subject to lateral movement and therefore can concentrate better on the object approached; and, secondly, a part of the body is always stationary. This latter is important with snakes that are patterned in brightly contrasting colors, since the moving part of the body has a confusing effect of disappearance, while the stationary part fixes the attention on that very stationary quality, giving an illusion of safety to the prey.

I have seen rattlesnakes use the concertina method in the field when approaching a questionable object, although I have never had the good fortune to see one stalking prey.

Gray (1946, p. 110) has shown that the concertina method is employed whenever a snake is confined within a narrow channel, whether it be straight or circular.

Under such circumstances the lateral waves are used to engage the walls of the channel and thus afford an anchorage, regardless of how smooth the walls may be. The engaging waves are made to travel backward (Gray, plate 5; Leutscher, fig. 1), thus causing the snake to advance. It may be noted that, when so confined, the concertina waves are not restricted to the central part of the body, but travel rearward from the head to the tail.

Tests on rattlesnakes indicate that they use concertina propulsion under two sets of circumstances. The first is in the open when there are no restraints, but where a slow, although definite, advance is sought. Under these conditions rectilinear motion is usually preferred to concertina, which is likely to be employed only if the advance be intermittent.

The second circumstance involves restraints, either in terms of a smooth substratum or restrictive side walls. On a smooth surface, on which traction is difficult to obtain, the snake takes instinctive advantage of any means of increasing the surface contact, such as by pressing side waves of its body against adjacent walls. Thus, if it be traveling along a narrow channel between vertical walls, it will widen its side loops until they engage both walls, and, by this side bracing, it will anchor one part of the body, so that the anterior may be thrust forward, or the posterior drawn up. This is, in effect, concertina propulsion, but the loops are far from regular. Sometimes a single central loop may be used; at others there may be one at head or tail, or both may be manifest at once. But there is no regular wave motion rearward, as Gray found in the common European grass snake; rather, there is a mixture of the concertina and rectilinear methods as the snake strives in every way to get a purchase on its surroundings. In fact, it is not necessary that a rattler be confined between narrowly separated parallel walls to produce concertina motion; if it be moving along the angle of a single wall and it finds the ground surface too smooth to facilitate rectilinear motion, it will throw side loops against the wall, seeking to increase the traction by taking advantage of any roughness in that wall. Thus a rattler moving along a wall sometimes uses a combination of rectilinear and concertina propulsion. But if the ground be rough, pure rectilinear progression is normal, if the confining channel is narrow. If there be no side restraints, the snake will use either horizontal undulatory or rectilinear locomotion, depending on whether it is in a hurry or advancing more deliberately. The sidewinder, under similar circumstances, will also vary its style to suit its pace, except that it will sidewind instead of undulating. If confined in a channel, it will use a combination of the concertina and rectilinear methods just as do the other rattlers. Mosauer (1933b, p. 15) noted that sidewinders in the field used concertina motion when sluggish and starting to prowl. Stewart (1933, p. 468) also observed that concertina crawling was used by a snake in a narrow channel.

These experiments with surfaces indicate that rattlers probably use concertina progression in their explorations of mammal holes, throwing out side loops to engage the walls whenever the ground is too smooth or soft to facilitate rectilinear progression.

#### RATTLESNAKE SPEED

The speed with which rattlesnakes can travel might be thought to be of importance in connection with the snake-bite problem, as a criterion of how successful one

might be in escaping from an attacking rattler. Actually, they so rarely attack, and they move so slowly—this refers to their crawling, not striking—that no one with his wits about him would have the slightest difficulty in evading a rattler moving at its top speed.

The persistence of an erroneous idea in natural history is exemplified by the way in which the notion that rattlesnakes are swift-moving was carried down through book after book. A statement to that effect was originally made by Hernández, in the first extended account of the rattlesnake ever printed (1615, fol. 192<sup>r</sup>), wherein he says that the rattler moves over rocks and precipices at great speed, and that the Mexicans called it *ocozoatl* after a wind. There was probably dual confusion here—first, between the rattler and some more speedy, racer-like snake; and, secondly, because one of the greatest of Mayan deities, Quetzalcoatl, the bird-serpent, had alternative names signifying the air and the rattlesnake. From these misunderstandings of what the Mayans told Hernández, and what he sought to convey, there was evolved the idea that rattlesnakes move with the speed of the wind—that they seem literally to fly—and we find this synthetic thought carried down through the subsequent editions of Hernández (1628, 1651, p. 329), and from him to Nieremberg (1635, p. 269), Piso (1648, p. 41), Jonstonus (1653, p. 26), Grew (1681, p. 51), Nieuhof (1732, p. 713), Owen (1742, p. 91), Dobrizhoffer (1784: see 1822, p. 287), and Clavigero (1787, vol. 1, p. 59). Eventually, Kalm (1752–53, p. 318) stated that he thought these reports of the great speed of the rattlesnake must have resulted from confusion with some other snake; and, from his time on, the idea gradually lost favor, although still given some support in new accounts by Silliman (1820, p. 229), and by Audubon (1827, p. 22), who claimed he saw a rattler chase a gray squirrel and gain on it. Goldsmith (1774, vol. 7, p. 212), although usually credulous in matters of this kind, took a doubtful view. Bartram (1791, p. 221; see also Daudin, 1801–4, vol. 5, p. 301), expressed the opinion, based on his own field observations, that a rattlesnake could move no faster than a man or child could walk, which is substantially correct. Since then, accounts of rattlesnake speeds have been more realistic, although Meek (1946, pp. 11, 51, 262) revives several of the ancient fantasies regarding rattlesnake speeds, including the tale of the rattler that outdistanced a man on horseback.

It is now known that rattlers, at their highest speeds, would have difficulty in attaining 3 miles per hour, even for short distances; in other words, their top speeds about equal a man's moderate walking pace. The most complete tests made to date to determine snake speeds were those of Mosauer (1935a, p. 7; 1935b, p. 24), in which he found that sidewinders attained 2 miles per hour and judged they might rarely reach 3 miles in short lunges. Although all other rattlesnakes use the horizontal undulatory method of crawling when they are anxious to make the greatest possible speed, there is no reason to believe, based on observations by Mosauer of slimmer, faster snakes, that any rattler can exceed the speed of a sidewinder.

While rattlesnake speeds have now been reduced to a credible basis, those of other snakes are still in the realm of controversy. The quickness with which a pursued snake can change its direction, and the ease with which it can dart between obstructions that block pursuit, are probably the genesis of some of the fantastic stories of snake speeds, notwithstanding Mosauer's tests (1935, p. 6), which

showed that the red racer (*Masticophis flagellum piceus*), certainly one of the swiftest snakes in the United States, reached a maximum speed of only 3.6 miles per hour. He thought that under exceptional conditions, for short lunges, a speed half again as great, or 5.4 miles per hour, might be attained by this slim and active snake. But statements that these snakes—and, indeed, slower ones—can travel as fast as man, or even a horse, can run, have appeared in print for many years, and still do (Grew, 1681, p. 48; Rolker, 1905, p. 207; Brendle and Unger,<sup>22</sup> 1935, p. 200; Fraser, 1936–37, p. 80; Stimpson, 1946, p. 165; De Lys, 1948, p. 78; Allison, 1948, p. 113). Nowhere has the controversial nature of snake speeds been better exemplified than in a series of communications appearing in *Country Life* (London) in 1944. The argument was started by F. R. Perkins (1944, p. 296), who inquired as to the maximum speed of the mamba, an agile and dangerous African snake. Before the discussion ended, almost a year later, the following had participated: M. A. Smith, p. 428; Waller, p. 428; Macleod, p. 516; Lowe, p. 516; Klapwyk, p. 516; Lane, p. 557; Breton, p. 604; Foran, p. 693; Macleod, p. 693; Ramsey, p. 780; Cailard, p. 825; Nash, p. 868; Rushton, p. 956; Renshaw, p. 1090; Hastings (1945), p. 121; and Kerrison, p. 122. The estimates of the speed of the mamba varied from a few miles up to 30 or more miles per hour. Most of the higher speeds were gauged by comparing the speed of the snake with that of a galloping horse—usually taken as being 30 miles per hour. Several observers claimed that a snake kept even with a horse at this speed, and, in one instance, even crossed in front of it. In no case was a distance measured or the snake timed as was done by Mosauer in his tests; this, of course, would be impossible with a dangerous snake like a mamba, but is merely mentioned to indicate the questionable nature of the evidence. There is no reason to believe that the speed of a mamba greatly exceeds that of a red racer. As to the results of the controversy in *Country Life*, it may be assumed that each participant “evermore came out by the same door wherein [he] went.”

With regard to snake speeds, it should be observed that the creatures suffer from a number of physiological handicaps and deficiencies, quite apart from their lack of legs. Rodbard (1948, p. 414) has pointed out that even at the most favorable body temperatures, poikilotherms such as snakes are capable of high degrees of activity for brief periods only; this limitation follows from the physiological effects of their three-chambered hearts and the pulmonary shunt, which do not permit the development of high blood pressure in the systemic circulation, thus denying adequate nourishment to the tissues to meet peak-load demands. And in the snakes this is accentuated by the attenuated habitus, which has led to the suppression or near suppression of one of the lungs. Muscle energy storage is quite limited. Mosauer (1935a, p. 7) observed how quickly the snakes in his tests tired. Malcolm Smith (1944, p. 428) and Bogert (1946, p. 148) have both expressed doubts concerning the high and sustained speeds supposed to be attained by certain snakes because of these important physiological handicaps. There is another difficulty of energy balance that must not be forgotten. Muscular energy operates at an efficiency of about 20 per cent (Martin, 1930, p. 617); therefore, about 4 times as much energy must be dissipated in the form of heat in a moving creature as is useful in producing movement. This would be a serious handicap to an animal having no

<sup>22</sup> Not held seriously by these authors; only given as an example of Pennsylvania German folklore.

sweat glands or other perfected means of cooling by evaporation, to say nothing of having almost no surplus water. And it should not be forgotten that the sinuous course of a snake's path involves a further disadvantage, since the snake must travel from 25 to 50 per cent farther than the straight-line distance in order to reach its destination. The body of a snake reputed to be traveling at 30 miles an hour, really would be moving at 40 or more.

Snake-speed tests are difficult to carry out in a satisfactory manner, which is why so few valid data are available. It is almost impossible to cause a snake to proceed directly from one point to another at its best rate of speed. If chased, or kept continually frightened in order to keep it at top speed, it will dodge and feint, endeavoring to escape by craft rather than by speed. And a venomous snake, such as a rattler, if it is being overtaken, will pause, throw itself into a defensive coil, and endeavor to save itself by intimidation, backed by a readiness to strike. This causes the failure of such demonstrations as the well-advertised "rattlesnake derbies." Stimpson (1948, p. 116) reported that in one such test in 1939 the winner ran the 30-foot course in 12 minutes and 12 seconds, or at a rate of a mile in about 1½ days.

#### MISUNDERSTOOD FEATURES OF CRAWLING

In addition to the exaggerations of speed, and the misinterpretations involved in rib-walking and the function of the ventral plates in the several kinds of locomotion, there have been other conclusions involving errors or exaggerations.

Thus Hutchinson (1879, p. 529) believed that snakes could ascend smooth surfaces by erecting their abdominal scutes as hooks, or using them to produce an adherence in the manner of the toe pads of some geckos.

Chateaubriand (1856, p. 112) stated that a rattler could stand on its tail and move along with the body held perpendicularly. This is only an exaggeration, for it is true that a rattler can move with the anterior part of the body raised well off the ground. Just as a rattlesnake can merge one type of crawling into another, so also it can quickly change from a crawling position to one of defense. Characteristically, one can crawl while assuming a defensive attitude, raising the anterior part of the body and facing an intruder, while the posterior part propels the snake backward or sideways toward some refuge or concealment.

A prowling rattler, if it has detected prey near at hand, will sometimes raise the head and neck well off the ground, while the body progresses by the horizontal undulatory or the concertina method.

McDaniel and Taylor (1877, p. 75) relate that a successful bite causes a rattler to change its method of crawling. Two people who had been bitten noted that the rattlers scampered away with every manifestation of delight at what they had done, and progressed in vertical waves. One may hazard the guess that these victims had been fortunate in imbibing the standard Western snake-bite remedy in advance of the accident.

I have already mentioned, in connection with horizontal undulatory progression and rectilinear progression, an ancient misunderstanding with regard to the use of vertical loops in these normal methods of crawling. It is sometimes not appreciated how much more limited is vertebral flexure in a vertical plane as compared with the horizontal. Snakes can make much sharper bends laterally than vertically

because of the nature of the interlock between adjacent vertebrae. Tests on freshly killed, fully relaxed rattlers showed the following minimum vertebral curvatures (all dimensions in mm.):

Subspecies	<i>C. v. oregonus</i>	<i>C. r. ruber</i>
	(mm.)	(mm.)
Length over-all.....	680	1,385
Minimum radius, lateral .....	20	50
dorsal.....	53	150
ventral.....	47	128

By “dorsal” is meant the minimum radius of curvature assumed by the spinal column when the snake is suspended by the head and tail with the dorsum upward; and “ventral” with the ventrum upward. It is evident that a rattler can make much sharper bends laterally than vertically.

Snake Tracks

Much of interest can be learned by a study of snake tracks, particularly in sandy, desert areas where they may be followed for long distances without a break. Indeed, professional collectors in such areas, setting out early in the morning before the wind has obliterated the tracks, use them as the principal means of locating their quarry.

From the track, an experienced collector can determine, with moderate accuracy, the kind and size of the snake that made it. He can follow its night wanderings and learn much respecting its habits. The direction an undulatory or sidewinding snake has taken is easy to discover; and even a snake proceeding by rectilinear progression will revert to the other methods often enough to reveal its direction by telltale piles of sand or at least will drag indicatory accumulations of sand into any natural depressions in its path.

SENSES

It is difficult to determine how any creature appraises its surroundings, and to what particular sense some reaction may be attributed. We are likely, unconsciously, to put ourselves in the animal's place and to consider which of our senses, under similar circumstances, with their relative human acuities, would most perfectly advise us of our surroundings. And this is further complicated by our tendency to expect the same response from a sense impression that would be induced in ourselves, as evaluated by our human intelligence and actuated by our human interests and reactions. Thus, our interpretations tend to be subjective rather than objective; and we are especially liable to inaccurate conclusions in the case of the rattlesnakes, which are equipped with an extra sense—the facial pit—the character of whose impressions brought to the brain we have difficulty in imagining. Only tests that involve blocking off all but one sense at a time, permit us to judge the acuity and field of operation of each sense separately, and such experiments introduce the further complications of unnatural conditions. Several tests of this kind

have been made, and we are now beginning to have some selective data on rattlesnake senses, but much remains to be done. In general, it is the conclusion that the vision of the rattlesnake is moderately good, but with narrow spatial limitations. Hearing is absent, but is partially replaced by a high sensitivity to tremors of the substratum upon which the snake rests. The sense of smell is acute, although operating in part with a mechanism different from our own—a mechanism that combines smell and taste. Touch is sensitive, but, as the snake has no tactile limbs, not particularly valuable. Finally, there is the pit, a high-temperature differential-receptor that gives the rattlesnake a knowledge of the direction and distance of objects whose temperature is higher than the rest of the surroundings, a valuable organ to a creature living largely on warm-blooded prey.

With these difficulties of interpretation it is not surprising, nor does it cast doubt on their powers of observation, that my correspondents differ widely as to the relative sharpness of the several senses of the rattlesnake. The following are example conclusions:

The sight of the rattlesnake seems to be very poor. The hearing, or the receipt of some vibration, seems to be their most effective sense. *Nelson S. Stone, U. S. Forest Service, Camp-tonville, Calif.*



I don't think that the rattlesnake's senses of smell, sight, or hearing are very acute, as a person must get very close to one before it shows alarm. *W. J. Petermann, U. S. Forest Service, Meeteetse, Wyo.*



Rattlesnakes seem to have fairly acute senses of hearing and eyesight, as they will generally be moving away when you first see them. I have no idea whether they have a sense of smell. *Kermit Miller, U. S. Forest Service, Libby, Mont.*



I believe the rattler's senses of sight, hearing, and smell are acute under favorable temperature conditions. All senses and movements are sluggish when they are cold. *B. A. Goodman, U. S. Forest Service, Stanford, Mont.*



The rattlesnake possesses a keen sight and appears to see everything; the hearing seems to be dull, while the sense of smell appears to be keen. *G. B. Clark, U. S. Forest Service, Duffield, Va.*

As one watches a rattler in his best defensive pose, one can readily appreciate these divergent opinions. Of the snake's absorbed scrutiny there can be no question; he is appraising your every movement and intention. But the determination of the senses by which he is making these judgments is not easy. He must be looking at you, yet, curiously, you will see that his eyes are not focused forward but are apparently looking sideways. He is taking deep breaths, but is this for the purpose of smelling, or is the resulting hiss the objective? His tongue is alternately extruded and withdrawn; and while protruded is sometimes held vertically upward, and sometimes vertically down, but always with the quivering tips widely divergent. What is the purpose of this spectacular maneuver? What form of radiation, airborne vibration, or floating particles are being intercepted? In an endeavor to answer these questions we shall consider the senses separately.

## SIGHT AND THE EYE

The eye of the rattlesnake has always had a fascination for people, particularly because it was, indeed, thought to be the source of the snake's ability to fascinate animals by those who have conceded it that mystical—and mythical—power. To many people the eye has a sinister appearance, a result, no doubt, of its fixed and unwinking stare, the narrow, catlike pupil, and the effect of the overhanging scale—the supraocular—that gives it a scowling and beetle-browed aspect (figs. 2:78 to 2:80). Many early writers found every evidence of malignity in the rattler's glance. Catesby (1731–43, vol. 2, p. 41) states that the eye is red; Kalm (1752–53) says no artist can depict the burning anger of its eye; Goldsmith (1774, vol. 7, p. 213) describes it as shining like fire, as the snake levels its dreadful glare upon its prey; Anbury (1789, p. 230) writes that the rattlesnake has a quick and piercing eye; Bartram (1791, p. 267) says that, when it is threatening an enemy, the eyes become as red as flaming coals; Winterbotham (1795, p. 406) says that in defense the eyes flame in a most terrible manner; Bosc (1803, p. 550) mentions their great brilliance; Ashe (1808, p. 142) observes that they glared fire as a snake faced his dog; Wakefield (1819, p. 74) says the eyes are red; Doddridge (1824, p. 81) likens them to balls of fire; Murray (1829, p. 316) says they are as red as flame when the snake is prepared to strike; while T., N.A. (1882, p. 6) notes that the eyes of a rattler blazed with fury when a stone was thrown at it. O. W. Holmes, in *Elsie Venner* (1861, vol. 1, p. 238), presents a classic description of a man paralyzed by fear when he saw a rattler's eyes shining in the darkness of a cave. Flack (1866, p. 324) warns hunters to beware of the rattler's hypnotic eye. Orcutt (1891, p. 190) refers to the magnetic influence of the rattlesnake's eye. Menger (1913, p. 147) says the eyes glitter like fiery red balls.

Several writers remark on the dilation of the eyes when the creature is angered: Foot (1807, p. 119) that it projects the eyes to a large size; and Hopkins (1930, p. 87) that, in exerting its mesmeric power, it dilates its eyes to the size of a 10-cent piece. T. (1887, p. 552) summarizes its fearful quality when he says that the eye is so dreadful no one can look at it for more than a moment. The mythical use of the eye in fascinating prey has been mentioned elsewhere (p. 1220).

But all of these writers are, in fact, concentrating into an imagined appearance of the rattlesnake's eye, the sinister threat of the snake's defensive posture. For the eye is singularly inexpressive of the snake's feelings and deportment. Far from flashing fire, it remains virtually unchanged, whether the snake is asleep or threatening some trespasser upon its seclusion. The snake has no movable eyelids; the scale-sheathed skin that surrounds the eye has neither the power of dilation nor of other voluntary movement; the pupil itself has little range of lateral motion; and, finally, unless the snake be asleep, the pupillary opening is responsive only to the incident light. So the expressiveness of the eye that we are likely to attribute to other creatures, because we observe it in ourselves, is certainly not evident in rattlesnakes.

As to the acuity of a rattlesnake's vision, there have been many guesses by observers, but there have been the usual difficulties in segregating the effects of the several senses to learn which one has produced some particular reaction that may have been noted. This is especially the case with pit vipers, such as rattlesnakes,

since they have two organs—eyes and facial pits—responsive to radiation. Brickel (1737, p. 142) thought rattlesnakes to be sharp-sighted. Some of my correspondents, as a result of their field observations, believe rattlers to have good vision, but only at close range, and this seems to be a sound conclusion.

Other correspondents bring out the fact that rattlers are especially responsive to moving objects:

It has been noted that rattlers seem to be very nearsighted, and depend on the movement of an object to locate it. *John H. Stanley, U. S. Forest Service, Andrews, N. C.*



Rattlesnakes do not appear to become alarmed unless a moving object comes within a few feet, or something actually touches them. *E. L. Thompson, U. S. Forest Service, Cascade, Idaho.*

The same idea regarding the importance of motion has been expressed by Kunzé (1879, p. 311), Rice (1895, p. 389), Beyer (1898, p. 23), Matteson (1899, p. 665), Bevan (1923, p. 163), Strecker (1927, p. 6), and Gibson (1940, p. 25). Reichert (1930, p. 262) experimented with a western diamond rattler (*C. atrox*) and found that it followed hand movements up to distances of 10 feet. Walls (1942a, p. 344) makes the following comment on the necessity of movement to visual recognition by reptiles in general:

Not only amphibians, but most snakes, lizards, and many carnivorous turtles appear not to see motionless prey. Motion is particularly important to diurnal snakes, whose visual acuity is probably the lowest of any diurnal vertebrates—*Dryophis* being a conspicuous exception in its ability to secure motionless prey solely by sight. Other diurnal snakes "lose contact" with the prey if it stops moving or freezes, and then attempt to regain rapport through olfactory exploring or trial-and-error tonguing. Nocturnal snakes, many of which have superb olfactory powers, are better able to locate and strike motionless prey, without need of vision.

My own tests, under moderate illumination, such as that from a north sky without direct sunlight, indicate that a rattlesnake can detect movements by sight alone at distances of 15 feet at least. These experiments were made on a nervous snake housed in a glass jar. Such a snake is particularly useful in tests of this kind since it will react to external stimuli by rattling, whereas after it has become accustomed to captivity, it will make no such response. By the use of a piece of white paper on the end of a thin rod that could be made visible to the snake through a door, it was easy to ascertain under what circumstances the snake became aware of the paper. No other sense but sight—not hearing, smell, the pit, or air motion—could possibly have been effective in causing this glass-encased snake to rattle. Yet it did rattle whenever the white paper was brought within its range of vision, although not always before the paper was waved about.

The distance at which a rattlesnake becomes aware of a moving object gives only a partial answer to the question of the effectiveness of its eyesight. We should like to know more of the acuity of sight under different conditions, and to what extent sight is important in securing prey and other objectives. Here the separation of the effects of other senses becomes more difficult, and adequate experiments more complicated. Noble and Schmidt (1937, p. 286) found that rattlers deprived of both pits and tongue were able to catch mice by sight alone. With cold-blooded

prey the pits would be of little use in any case. But even with all their senses intact, it is surprising how frequently captive rattlesnakes are seen to miss their prey when they strike at it, even at close range. So although we have little doubt as to the importance of sight in rattlesnake activities, tests show the eyes to be far from perfect instruments.

Our inadequate experiments with the eyes may be partially supplanted by studies of eye structure and operation. This involves an estimation of the probable effectiveness of the snake's eyes from the known principles governing the visual perceptions of better-known creatures.

In this connection G. L. Walls, in a number of important papers, has discussed various features of eye structure; those that include data on snakes are as follows: 1931, colored lenses; 1932a, visual purple (rhodopsin); 1932b, pupil shapes; 1933 (with Judd), color filters; 1934a, the retina; 1934b, the spectacle or brille; 1938, eyeshine; 1940, phylogeny; 1942a, general; 1942b, visual mechanisms.

Walls finds, first, that the eyes of snakes differ so radically from those of lizards, with the development of new solutions for old necessities, that he concludes that the ancestral snakes, after breaking away from their lizard forebears, must have passed through a period of fossorial or subterranean existence, during which the serviceability of the eye was greatly reduced, much as it is in the worm snakes of the genus *Leptotyphlops* today. Upon its revival as an important and useful organ, some of the features of the lizard eye that had been lost through degeneration were not restored—evolution in such cases being thought irreversible—and other expedients serving the same purpose were developed in their stead. As an example, the yellow oil droplets at the bases of the retinal cones in certain diurnal lizards were, in some diurnal snakes, supplanted by a yellow color in the lenses. Both of these methods of narrowing the spectrum of the incident light result in greater acuity through the prevention of chromatic aberration.

Certain generalities with regard to the eye structure in snakes are of interest. No snake<sup>23</sup> has a fovea, or retinal center of high sensitivity, hence there is no fixation or precise aiming of the eye at objects (Walls, 1942a, p. 292). In most snakes the eye sockets are so far back on the sides of the head that the range of possible stereoscopic vision is limited to a very narrow field directly in front of the snake. For both of these reasons eyeball movement is a relatively unimportant feature of eye usage.

Distance accommodation in snakes is secured by motion of the lens toward, or away from, the retina, rather than by the more customary change in lens shape (Walls, 1940, p. 7). The snake eye has a hard, transparent, lenslike covering—the spectacle or brille—the genesis of which has been discussed by Dixon (1902, p. 990), Neher (1935, p. 533), and Walls (1934b, p. 1045; 1942a, p. 454). The spectacle is valuable as a protection to the eye; and, because of its optical effects on the eye, has had an important bearing on the structure itself. The spectacle is shed periodically with the rest of the snake's skin. The eye covering in a shed skin is clearer, stronger, and stiffer than the other elements of the skin. It often shows scratches and abrasions prior to shedding; and, at one period of the shedding process, there is a milky fluid between the spectacle and the eye that considerably interferes with sight. The few lizards that lack movable eyelids have spectacles like those of snakes.

<sup>23</sup> Except *Dryophis mycterizans*.

As to the derivation of the particular group of snakes to which the rattlers belong—the pit vipers or crotalids—Walls (1942a, plate 1; 1942b, fig. 1) pictures the ancestral crotalid as having been derived from a primitive diurnal colubrid; the changes in the eye, particularly the vertical pupil, the absence of any color filter, and the partial suppression of single and double cones in favor of rods in the retina, have resulted in an organ more suitable for nocturnal activity than was the ancestral type from which it was derived. Dim-light vision is made possible by retinal rods containing visual purple. Their high sensitivity requires a slit, rather than a round pupil, since the former is more susceptible to contraction and almost complete closure, as is required by a nocturnal animal in daylight, if complete dazzling and virtual blindness are to be avoided. Walls' theory of snake phylogeny, as deduced from eye structure, has been discussed by Bellairs and Underwood (1951, p. 211).

The most obvious external characteristic of the rattlesnake's eye is the vertical pupil. This shape of pupil, although often thought characteristic of poisonous snakes, is, in fact, quite independent of a snake's venomous quality; as has been stated, it is more an indication of nocturnality than anything else, although it is not a universally accurate criterion even of this feature of snake adaptation. For example, the shovel-nosed snake (*Chionactis occipitalis*), certainly a nocturnal species, has a round pupil.<sup>24</sup> In some snake families the shape of the pupil is constant, regardless of whether an individual species prefers daylight or nighttime activities; but, in other families, the diurnal snakes usually have round pupils, and the nocturnal, elliptical, or at least oval. But, after all, there is really no sharp boundary between nocturnal and diurnal snakes, for they are so greatly influenced by temperature conditions that they may be nocturnal at one time of year and diurnal in another; or, within a single species, the residents of higher, cooler areas may be abroad in the daytime while those found in the deserts below are necessarily restricted to activity at night. This is the case with the rattlesnakes; for, despite the fact that the elliptical pupil and other structural characteristics of the rattlesnake eye show it to be particularly adapted to nocturnal use, rattlesnakes are far from being exclusively nocturnal. It is not even to be supposed that they see better at night than in the daytime, for they do not; they are merely equipped to respond better to the limited radiation available at night than a diurnal animal would be. In other words, their night vision is proportionately better than the night vision of a diurnal animal, but in either case the night vision is imperfect when compared to that under conditions of daylight.

As we consider the actual serviceability of the sense of sight to rattlesnakes, we observe that it might be used to guide them toward three primary objectives: mates, food, and protection. But for the first of these the rattler is probably dependent on other senses, smell particularly. As to the second, the rattlesnake is a slow-moving creature; and although he occasionally trails his prey (see p. 616), he is much more accustomed to lie in wait for it, or to seek it down holes. The ambushing rattler, then, needs sight to aid him only in detecting and striking prey but a few feet away, and in this he has the assistance of the facial pits, if the prey be warm-blooded.

<sup>24</sup> For accuracy, the shape of the pupils of snakes must be observed in life. Preservation often distorts the shape of the pupil.

As to protection from enemies, whether birds or mammals, the rattler is too slow to outrun or dodge even the slowest of them, hence a superior or long-range sense of sight would not be important in the detection of danger, except that it might warn him to avoid discovery by freezing. For a rattlesnake's escape must first be dependent on concealing coloration; and, if this fails, on a noisy and threatening posture while in retreat, backed up by the venomous strike. Here again he has need only for short-range vision, particularly responsive to movement. So it would appear that the purposes for which a rattlesnake might use his eyes bear out the supposition that the range of vision is relatively short.

Although it is difficult to determine the response of rattlesnakes to visual stimuli—that is, the extent to which their reactions are affected by what they see—it is not difficult to observe the ways in which their eyes operate.

Most obvious of all is the effect of incident light upon the iris opening, which is narrow in bright light and wide in dim. There is some independence of action between the eyes; if we start in dim light with the pupils moderately dilated and shine a light directly into one eye, so that the pupil is reduced to a thin slit, the other will respond also, but by no means to the same degree, for it will usually adopt an intermediate opening. Responses to light are quite rapid; it takes but a second or so to change from wide opening to a narrow slit. The closing of the pupil in the face of increased light is more rapid and positive than the reopening after the light source has been removed. A captive snake will almost never move its head as if the beam of light caused discomfort; the only evidence is the immediate pupillary contraction.

There are some species differences. The sidewinder (*C. cerastes*), undoubtedly the most consistently nocturnal of rattlesnakes, has a wider pupillary opening than such other species as the red diamond (*C. r. ruber*) and the southern Pacific (*C. v. helleri*) under the same degree of illumination. Whether the sidewinder's pupil becomes completely round in absolute darkness, I have been unable to ascertain. It is almost round in very dim light. Similarly, the pupil of the southwestern speckled rattler (*C. m. pyrrhus*) is opened wider than that of *ruber* or *helleri* in the same light.

In rattlesnakes the pupil extends almost from the upper to the lower edge of the visible part of the eyeball. The pupillary borders are clear-cut and even. There seems to be no change in the major diameter of the ellipse upon contraction, there being only a change in the width of the opening. There are some specific differences. For example, the major axis of the ellipse in the southwestern speckled rattlesnake (*C. m. pyrrhus*) occupies a smaller vertical section of the visible eyeball than is the case in either *ruber* or *helleri*.

When a rattlesnake is asleep, it apparently closes the iris to the minimum opening, and only a thin black line of pupil remains visible. That the snake is truly asleep, and not merely reducing the aperture to a point adjusted to the impinging light, can be proved by disturbing the snake without changing the illumination, whereupon the pupil will dilate. In fact, I have, on one or two occasions, awakened a rattlesnake by shining a flashlight beam into one eye, whereupon the aperture widened, notwithstanding the increased light intensity. A snake accustomed to captivity, if disturbed only slightly, will go to sleep again almost immediately.

The pupil of the rattler's eye appears black. The iris is flecked or punctated with colors, rather metallic in quality, generally in gray, brown, or yellow. There may, in fact, be an approach toward a pattern, a horizontal dark line across the iris being evident in the sidewinder. A study of the irises of some fifteen species shows that there is a definite tendency of the iris color and pattern to match that of the adjacent head so that the eye is made inconspicuous. For example, in the Omilteman small-headed rattler (*C. i. omiltemanus*) the upper half of the iris is light and the lower dark, exactly matching and forming parts of an upper light and lower dark stripe on the side of the head.

The eyeball has some range of horizontal rotation. Such motions are not easy to induce, as the snake does not ordinarily follow an object with the eye. The most effective way of producing motion I have discovered is to place a snake in a glass jar and rotate it slowly. The snake's eye will first attempt to compensate for this motion, and will then twitch back to its normal orientation. Thus, as the jar turns, one eye turns forward, the other back. The readjusting twitch is made in both eyes simultaneously.

The normal direction of the optical axis points slightly forward of an angle of  $90^\circ$  with the median line of the head; and the snake seems to have a greater power to rotate the eye forward of this normal direction than back. I should judge the rotational range of each eyeball (in a horizontal plane) to be only about  $20^\circ$ . In *ruber*, when the eye has been turned to any extent out of its normal position, an edge of lighter-colored eyeball may be seen. The two eyeballs can rotate independently, as can be demonstrated by watching one eye directly, while that on the far side of the head is observed in a mirror. Or, both eyes may be watched from directly in front, as the motion is induced.

If the head of a rattler be tilted up (or down) in front, the eye will rotate so as to keep the major axis of the pupillary ellipse vertical. The maximum tilt from the vertical is somewhat less than  $45^\circ$ ; if the head be tipped more than this, the pupil can no longer be kept vertical. If the tilting be in the nature of a side rotation—the left side of the head up and the right down, for example—the eye on each side will attempt to compensate for the rotation, by maintaining the optical axis of each eye as nearly horizontal as possible. Both of these reactions to tilting the head indicate that the rattler has a good sense of balance.

Eyeball motions cannot be brought about by bringing some object up toward the eye, either from the front or side, or even by touching it. The snake seems to place full confidence (if the anthropomorphism may be excused) in the ability of the spectacle to protect the eye, and does not flinch in any way as motions are made toward the eyeball.

When a rattlesnake is resting—that is, is not in the fighting pose or expecting food—it seldom makes an effort to keep any specific object in sight, either by rotating an eye or the head. I do not presume this to result from entire indifference, but merely that, lacking a fovea or spot of supersensitivity on the retina, the sight from one direction is about as good as another, provided the object is in a line through the pupil to some point of the retina. I have not noted any endeavor by the snake to take advantage of binocular or stereoscopic vision by turning its head to point the snout at a moving object, unless the snake be thoroughly aroused, and in this case it may be bringing the other senses to bear, as much as

sight. There is no effort to direct the ocular axes forward when there is a moving object in front of the snake's snout. At best, the range of stereoscopic vision must be very narrow.<sup>25</sup> As one looks at a rattlesnake's head, end-on at a distance of a few inches from the snout, only a narrow slit of each pupil is visible, and one wonders whether the observer's eye is in the line of vision of the snake at all. Only a slight motion of the observer's eye to the right or left will cause one of the rattler's pupils to disappear around the bulge of the eyeball or behind the pre-ocular scales. But in any case, the snake seems little interested in stereoscopic vision, monocular being adequate. One test, indicating that the snake does have stereoscopic vision even though the pupils are directed outward, is to shine a flashlight at the snake's snout from directly in front. Although the light strikes the eye at almost 90° from the optical axis, it will cause the pupils to contract, thus indicating that light from the front does reach the retina. These remarks have reference to a rattlesnake in its resting position. A rattler in a defensive or striking coil does face the object of its displeasure, but this is probably more for the purpose of being able to strike directly forward than to secure the benefits of stereoscopic vision.

Walls (1942a, p. 342) calls attention to the method by which some reptiles wave the head from side to side in order to get impressions of an object directly ahead in each eye alternately. I have seen this done by a sidewinder (*C. c. laterorepens*).

Duncan (1939, p. 14) describes the methods of Ross Allen, who believes that rattlesnakes cannot see directly overhead. It was his practice to wave his right hand before one to attract its attention and then to seize it behind the head with his left, bringing the hand in from above and behind. It is generally believed that a rattlesnake cannot strike upward, but this is not true.

We may safely conclude that Anon. (1858a, p. 327) was the victim of a campfire tall tale when he reported that rattlers could discern a vulture or falcon passing overhead, and take refuge; or that rattlers were seen prowling about with the head cocked sideways on the lookout for birds' nests in the trees. Stebbins (1954, p. 334) has discussed the ability of snakes to focus their eyes on some object.

Rattlers, like some other snakes, have eyeshine at night. It is by no means so evident as in many mammals, and, owing to the narrow pupillary opening, is only visible from a point near the line of the optical axis. I have seen it only experimentally with a flashlight, never under natural conditions in the field, although I have come up to many rattlers on the road at night with the headlights of the car shining on them, under conditions that would have made a cat's eyes visible at a hundred yards or more. The reason for eyeshine—a particular character of the retina whereby dim-light vision is intensified—has been discussed by Walls (1938, p. 103). Lacépède (1788–89, vol. 2, p. 393; Kerr, 1802, vol. 4, p. 248) early mentioned eyeshine in some snakes, rattlers not being specifically included. He thought it a kind of phosphorescence—that is, the emission of light stored during daylight. The extent of eyeshine in various creatures has been discussed by Walker (1939, p. 349). He cautions against the confusion of eyeshine in snakes with a mere reflection from the spectacle (p. 353).

Michler (1857, p. 121) says that the glare of a fire one night on the Mexican border attracted a large number of rattlers. I know of no reason to believe that

<sup>25</sup> Walls (1942a, p. 292) states that the binocular angle of most snakes varies from 30° to 40°, the limits in the species so far investigated being 20° to 46°.

rattlers, being to a considerable extent nocturnal, are in any situations phototropic. Possibly, if the observation was accurate, the rattlers might have been attracted by the heat of the fire. Cowles observed a sidewinder that had to be restrained to prevent its crawling into a campfire.

The fact that the skin or spectacle covering the eyeball of a snake is semiopaque during a part of the period antedating skin-shedding may account for some of the old-time descriptions of winking snakes, or snakes sleeping with their eyes closed. Bartram (1791, p. 269) described a rattler met on the trail that had half-shut eyes; and Tyson (1683, p. 27) thought that the eye might be cleaned by a nictitating membrane, an idea repeated by Bosc (1803, p. 550), Rees (1819, p. 1), and Reid (1889, p. 227).<sup>26</sup> Charas (1670, p. 14) thought that vipers have eyelids. But, of course, no snake has movable eyelids or a nictitating membrane of any sort, although the present immovable spectacle or brille is now known, from embryological studies (Neher, 1935, p. 533; Walls, 1942a, p. 454), to be a development of what was once a lower eyelid.

It is doubtful whether a rattlesnake is in any way influenced by color in the acceptance of prey. Captive rattlers show no preference between gray and white mice; in fact, mice artificially colored blue, green, yellow, and red were readily accepted at the San Diego Zoo.

Summarizing our knowledge of the rattlesnake's eyesight, we may conclude that it is fairly good at close range and is particularly responsive to moving objects. The structure of the eye shows it to be relatively more perceptive in faint than strong illumination, that is, the rattlesnake is better able to cope with dim light than are most diurnal animals. It is probable that the eye affords a general impression of the surroundings rather than a sharp image of any particular object.

#### HEARING

Rattlesnakes, in common with all other snakes, lack external ears. There would seem to be a considerable difference of opinion among herpetologists as to whether or not snakes are deaf, such modern herpetologists as C. H. Pope (1937, p. 40), and Schmidt and Davis (1941, p. 60) maintaining that they are; whereas Gadow (1901, p. 583), F. Wall (1921, p. 467), and Malcolm Smith (1943, p. 4) state that they can hear quite well. Yet this apparent difference of opinion may be more a matter of definition than otherwise, for all agree that under certain circumstances snakes are made aware of external vibrations that are first carried by the air as sound waves, and are then transmitted to the substratum upon which the snake rests, for the snake is particularly sensitive to the faintest tremors of the substratum. Certainly, as far as rattlesnakes are concerned, they do not appear to be conscious in any way of the direct impingement on any part of the head or body of the types of air vibrations that we know as sound waves, although they may recognize air movements via the pit. But if the type of the substratum upon which the snake rests is in any way responsive to sound waves, as is the case, for example, with an ordinary wooden or fiberboard box, then the vibration is, in turn, transmitted to

<sup>26</sup> This misunderstanding may have been a matter of definition. Goldsmith (1774, vol. 7, p. 167) states that some serpents have only lower eyelids, whereas in others there is a nictitating membrane. But it should be remembered that in his day the legless lizards, some of which have eyelids, were thought to be serpents. Topsell's *Historie of Serpents*, 1608, included in this category, not only true snakes, but such diverse creatures as lizards, crocodiles, dragons, turtles, frogs, toads, salamanders, and newts. Bees, wasps, caterpillars, worms, scorpions, and spiders are also described, but they seem to be less certainly "serpents" than the reptiles and amphibians.

the snake, which is thereby alerted. This is not to suggest that snakes are only responsive to these foundational vibrations if the air serves as an intermediate avenue of their transmission; on the contrary, ground tremors emanating directly from the disturbing source are much more often the cause of stimulation.

That ground vibrations, rather than air-propagated waves, serve to warn rattlesnakes of the presence of an intruder has been observed by a number of my correspondents:

I think rattlers are more sensitive to feeling, probably through the ground, than to hearing, or even sight. *C. H. McDonald, U. S. Forest Service, Stevensville, Mont.*



Rattlers hear well when something strikes the ground, but don't respond so well to a call. *Ellen Johnston, U. S. Fish & Wildlife Service, Shelby, Mont.*



With regard to hearing, it is my belief that rattlesnakes are sensitive to vibrations, such as footsteps on the ground. *Calvin A. Bowman, U. S. Forest Service, Deer Lodge, Mont.*



I don't know whether rattlers hear sound, but a thump on the ground will surely be noticed. *Gustave W. Koski, U. S. Fish & Wildlife Service, Windham, Mont.*



A rattlesnake does not need to see you to know you are in close proximity; he is very sensitive to the vibration of the ground when you are approaching him. *Judge W. S. Owens, Cody, Wyo.*



Rattlesnakes apparently are sensitive to vibrations of the soil or rock for considerable distances. *Glen E. Sindel, U. S. Forest Service, Descanso, Calif.*

Published comments agreeing with these statements respecting the sensitiveness of rattlesnakes to vibrations conducted through the substratum have been voiced by Pike (1898, p. 38), Bogert (1941b, p. 337; 1945, p. 2), and Davenport (1943, p. 14).

The anatomy of the snake's ear has been discussed by Dixon (1902, p. 991), Gadow (1901, p. 583), Manning (1923, p. 241), Malcolm Smith (1943, p. 4), and Bellairs and Underwood (1951, pp. 216, 228). There is neither an external ear opening nor an ear drum. The residual auditory apparatus that snakes still retain comprises a slender bone—the stapes or columella auris—extending from the quadrate to the pro-otic, although the connection with the latter is rather loose (figs. 11:1 to 11:4). Whether this mechanism can be serviceable in the transmission of air vibrations of the kind that record the sensations of sound in our ears may be questioned, both on the score of anatomical evidence and experiment. Gadow (1901, p. 583) and Dixon (1902, p. 991) thought that the act of eating would produce a thundering sound in the internal ear. Manning (1923, p. 241) questions the usefulness of the mechanism as a part of an organ of hearing. Pope (1937, p. 40) believes that the stapes has lost its ability to transmit sound waves.

The evidence of such tests as have been made on the hearing of snakes would seem to confirm these conclusions. O'Reilly (1894, p. 70) showed that the rearing and "dancing" of cobras are caused by the swaying motion of the snake charmer and his flute, and not by his music. Experiments were made with a flute and a violin. There was no response upon the part of the snake unless the instrument was allowed to touch the snake's box and a low note was played; under these circumstances the vibration of the box could be felt even with the hand, so it was

not remarkable that the snake reacted. O'Reilly found that snakes danced to the movements of a snake charmer whether or not music was being played. He observed that feeding snakes were not disturbed by people's voices, but they were agitated if any motions were made.

F. Wall (1921, p. 467) experimented with cobras that had been blindfolded with tape and found them to be quite deaf to air-conducted sounds. With a stick, he beat tin cans held close to the snakes, but without response; nor did they react to the sound of a bugle. But the slightest tremor of the floor, the falling on them of rust particles from the can, or the impingement of the blast of air emanating from the bugle would cause the snakes to rise and spread their hoods.

Davenport (1913, p. 14) made experiments by violently shaking a can of rocks close to a snake. To this racket there was no response; yet when the can was placed on the ground with only the slightest bump the snake instantly became alert. He found snakes able to detect a light step at a distance of 15 feet.

I have caused a radio to play for long hours beside nervous rattlesnakes without their showing the slightest reaction, although they rattled immediately at any visible movement.

The most complete set of hearing experiments ever conducted on snakes—and these were principally on rattlesnakes—were those of Manning (1923, p. 241). Sounds of from 43 to 1,376 cycles per second were produced in a telephone receiver with sufficient intensity to have been heard by a human being at a distance of 100 yards or so. The snakes experimented on were eastern diamondbacks (*C. adamanteus*), timber rattlers (*C. h. horridus*), western diamonds (*C. atrox*), and pigmy rattlers (*S. miliarius*). Moccasins and copperheads were also used. The snakes were housed in cages that were covered with black cloths during the tests, the observations upon them being made through peep holes. Usually the tests were conducted with the telephone receiver hung 30 cm. (11.8 in.) above the snake's head, but in some experiments the instrument was suspended beside the snake's head, at a distance of only a few centimeters. The sound duration was usually 5 seconds. Two criteria were considered indicative of response—rattling and tongue protrusion. Anyone familiar with the behavior of freshly caught, and therefore nervous, rattlesnakes will agree that these are the reactions usually evident when a snake becomes conscious of an intruder, regardless of the sense by which it has been alerted.

The tests were almost universally negative; the snakes seemed quite deaf to these loud sounds, although they would instantly rattle at the sight of a person passing a cage. But there were occasions when some of the diamondbacks responded to the lowest of the frequencies (43 vibrations per second), and one exceptionally nervous *C. atrox* responded also to the next higher frequency (86 cycles). These tests were made with the telephone receiver beside the snake, and it is not impossible—as suggested by Pope (1937, p. 41)—that in these exceptional instances the vibration may have been perceived through the pit rather than the ear. Or the sound may have been energetic enough to vibrate the wooden bottom of the snake's cage; for Manning found, if a cage were rested on the sound-producing instrument, that the vibration (at the lower frequencies) would readily arouse the snake.

Manning stated that the remarkable sensitiveness of the snakes to visual stimuli, as compared to the lack of response to loud sounds, was the outstanding feature

of the tests. He concludes that rattlesnakes are deaf, in the usual sense of the word, and that no rattler ever heard another's rattle.

I made a series of experiments on a large red diamond rattler (*C. r. ruber*) that would rattle upon the slightest disturbance—it had been slightly injured in the course of capture—and therefore was a good experimental subject. The snake taught me how necessary, yet difficult, it was to eliminate the possibility of sense impressions reaching it by unsuspected avenues, before one could really judge whether it was susceptible to the direct air waves that we call sound. When I clapped sticks together, with my hands beyond its range of vision, it reacted, but I found it was watching the swinging of my feet beneath the table, for I was sitting on a high stool without a footrest; and when a screen was interposed it caught my movements reflected in a nearby window. It was so extraordinarily sensitive to ground vibrations that footfalls 15 feet away on a cement floor alarmed it, and this whether it rested on sand or on a blanket. Placed in a closed fiberboard box, and suspended by a rubber band from the center of a stick that in turn rested on a pillow at each end—a precaution against vibration reaching it through the suspension—it reacted quite readily to sounds of clapped sticks or a radio; but clearly these were transmitted through the box acting as a sounding board, despite the deadening quality of fiberboard. Placed in a muslin sack with the same support it failed to react, but I found it was because this bundling of its body seemed to cow it. Finally, I placed it in a Chinese basket formed of woven bamboo withes, using the rubber-band and pillow method of suspension. Again it showed normal sensitivity by rattling at the slightest movement seen through the weave of the basket or to the dropping of a few grains of sand on it from above. But the basket evidently failed to respond to air-borne sounds, and the rattler in turn did not react to clapped sticks or a very loud radio but a few feet away, provided the radio was never turned completely off; if it was, the rattler sometimes sensed the heating of the tubes when it was turned on. I eventually tried alternating the radio between silence and full power at a distance of only 6 inches from the snake's basket, and with the noise at times so loud as to be quite distressing to a person 10 feet away. Once or twice the snake reacted—to low notes, it seemed to me—but only hesitatingly and briefly; yet with this fearful clatter continuing, it would rattle violently if I came in sight, or touched the supporting crossbar, showing that it was still on the *qui vive*. I finally reached the conclusion expressed by others: that rattlesnakes are deaf to air-borne vibrations unless these serve to vibrate the solid material on which the snake rests or which a part of its body may be touching. To any vibrations so conducted the creature shows extraordinary sensitivity.

I do not think a snake's inability to sense directly what we call sound lies in its being susceptible to different frequencies than those that affect the human ear, notwithstanding the opinions expressed by some that snakes can hear high-pitched sounds (Corkill, 1932b, p. 4). Certainly the radio I used in the tests had a wide range. A dog whistle, operating at a frequency above what the human ear can hear, was without effect on my red diamond rattler. As to the low notes mentioned in Manning's and my own tests, I think these were sensed merely because they caused a mechanical vibration of the substratum when the higher tones did not.

The question arises as to whether a snake's sensitivity to substratal vibrations involves the use of the snake's residual inner ear. Wall (1921, p. 468) expresses the

opinion that it does, based on the ability of a person to hear vibrations in a solid, when the latter has been brought into contact with the bones of the skull. Bellairs and Underwood (1951, pp. 216, 228) share this belief.

Elliot (1934a, p. 507) thought that snakes sense ground vibrations by means of their rib tips. Payne (1945, p. 507) says that the ability to perceive vibrations in the substratum is provided by nerve endings in the epithelium, scales, and rib ends.

Tumarkin (1955, p. 221) has proposed a theory of ear evolution and use that involves a new hypothesis concerning the snake's detection of substratal vibrations. He concludes that the ophidian auditory apparatus is primitive, not the degenerate residue of a former air-borne-vibration detector; that from the first it was and remains an efficient apparatus for the detection of ground tremors. The sounds, in the form of substratal—not air-borne—vibrations, are conducted from the snake's lower jaw (in contact with the ground or other solid), via the articulo-quadrato joint and the stapes, to the snake's sensory center. If this theory is correct, and the undersurface of the lower jaw is an important link in the transmission of substratal vibrations, then any snake—a rattler or cobra, for example—sacrifices this sense when it raises its head to assume a threatening posture. Evidently hearing, in the form of the recognition of ground tremors, is important in alerting the snake to distant movements, such as the tread of a passer-by, but its advisory value is abandoned in favor of sight—and the pit, in rattlesnakes—upon the closer approach of the intruder.

With snakes so sensitive to vibrations of the substratum that they react to many kinds of sounds that we hear with our ears, it may seem almost academic to attempt to determine the means by which they become aware of the disturbances. But this is hardly the case, since the threshold of response is clearly dependent on both the character of the disturbance and the agency of transmission available, and it may be of some practical value to understand these in order to know the best means of frightening snakes away. The piping of a flute is not apparent to a snake, but on the other hand the tramp of a horse is probably sensed by a rattler long before it would be heard by a man, unless accompanied by the breaking of twigs. Tennent (1860, vol. 1, p. 196) and Fitzsimons and Fitzsimons (1932, p. 37) tell of the practices of various Asiatic and African peoples, in using a stick with a loose metal ring to warn snakes away, if they walk abroad in the night. DeWet (1929, p. 1036) says the Hindus wear sandals that make a creaking sound and also beat the ground with sticks. One would presume that thumping the ground with a heavy stick would be most effective, and the tinkling ring a useless ornament. Kincaid (1931, p. 66; Towne and Wentworth, 1946, p. 258) tells of a custom of Mexican shepherders who shuffle their feet because they believe rattlers won't strike a moving object, which, of course, is not true. But foot shuffling might be of some utility in alerting a rattlesnake through ground vibrations, causing it to rattle. Certainly a knowledge of the kinds of disturbances most readily sensed by snakes would be distinctly advantageous to anyone seeking to scare them out of his path, or to make them rattle so they might be avoided.

The fact that snakes have no external ears troubled the old-time naturalists, who could not conceive of their being deaf, at least to ordinary air-borne sounds. Charas (1670, p. 14) and Goldsmith (1774, vol. 7, p. 167) thought the nostrils served as ears as well. The so-called charming of snakes by music, practiced by sidewalk

entertainers in the Orient, has long been assumed to indicate their sensitivity to sound. Snake charming is a very ancient practice (Jeremiah viii: 17) and it is only natural that this supposed method of rendering them harmless by the soothing sounds of sweet music should have been extended to rattlesnakes upon their discovery in the New World. Said "Phil. Harmonicus" in 1741 (p. 200) "I have been credibly informed by a Person who has actually made the Experiment in America that the most venomous Rattle Snake will be overcome & intoxicated as it were by soft Music, as to stretch itself at full Length upon the Ground and continue in all Appearance without Life or Motion." This idea was repeated by Carver (1778, p. 483) and by Chateaubriand (1828, vol. 2, p. 163; 1856, p. 113; see also Martin, 1851, p. 238; Figuier, 1869, p. 85; Lewis, 1874, p. 260; and McDonnell, 1950, p. 330). Madame Calderón de la Barca (1843, p. 431) reported that the natives along the Mexican coast at Tampico could make rattlers come by calling them.

The question whether the snakes used by the Oriental entertainers in their "snake-charming" acts are really affected by the music has produced an extensive literature with a growing skepticism. Leighton (1892, p. 735) stated that snakes in the London Zoo reacted to violin music, noting changes in notes and tempo. Pike (1898, p. 38) thought snakes were fond of music, although admitting that it could be sensed only through vibrations of the substratum. Macht (1954, p. 81) revives the belief in the hearing powers of snakes, particularly cobras, yet adduces hearsay rather than tests to substantiate the claim. But, as has been shown by O'Reilly (1894, p. 70) and Wall (1921, p. 467), the cobras' response to the piping reed of the snake charmer is entirely a visual one; it seems to be swaying back and forth in time with the music, but in reality it is only following the movements of the pipe and piper. The cobra is the common terpsichorean participant in all such shows because its erect posture and wide-spread hood render its weaving attention to the piper so striking.

Doubt as to the effectiveness of music in pacifying or charming snakes is not particularly new, nor is the belief that snakes are deaf in any way novel. "They are like the deaf adder that stoppeth her ear" Psalms lviii: 4. Damiri, the Arabian encyclopedist of the fourteenth century, said it was an Arab belief that vipers are deaf (Jayakar, 1906-8, vol. 1, p. 632). This doubt as to the hearing ability of snakes, although now extended to all forms, may have been first attributed to some of the lethargic vipers of the Near East. Corkill (1932a, p. 606) states that the Levantine viper (*Vipera lebetina*) acts as if peculiarly deaf and blind.

Brooking (1934, p. 95) reported that Great Basin rattlers, far from being frightened by the noise and vibration of an air-compressor in a building, seemed to be attracted to it. It is to be presumed that they were seeking warmth or a refuge rather than noise.

To conclude: Rattlesnakes are deaf to the direct impingement of air-borne sounds, but are highly sensitive to vibrations of the ground or platform on which they are lying. If the latter vibrates in response to air-borne vibrations, the rattler will sense the disturbance.

#### THE TONGUE AND SENSE OF SMELL

As one approaches a snake in the wild, the first evidence that the presence of an intruder has been recognized is likely to be given by the tongue. The eyes are

without the possibility of expression or winking; there are no ears to cock forward. Instinctively endeavoring to remain undiscovered through its blending coloration, the snake will seldom move until it seems to detect that it has been noticed by the trespasser. And so the flicking tongue is the only outward sign that the snake has noted something amiss. Clearly the tongue is being employed in some way to investigate the stranger; to give some indication of his character and intentions. Until quite recently, the nature of the impression conveyed by the tongue and the course of its transmission to the snake's consciousness were unknown. Now the tongue is believed to be an adjunct of the sense of smell, although not the sole vehicle of that sense.

From the earliest days, the snake's delicate, bifid tongue has been a fruitful source of superstition and folklore. Aristotle believed (Peck, 1937, pp. 203, 395) that the tips of serpents' tongues were double in order that the snake might get a double pleasure from what it tastes. It was a myth of the ancient Greeks that Cassandra and other prophets secured their powers of divination through having their ears cleaned by the tongues of serpents; and one Roman cure for ulcers was to have them licked by the tongues of sacred serpents (Jayne, 1925, pp. 222, 411; Dawson 1935, p. 64). Fraser (1936-37, p. 82), noting that snakes used their tongues only when active, thought it might be to facilitate cooling by evaporation, in the manner of a dog; this would be virtually ineffective, as discussed elsewhere, because of the minute surface of a snake's tongue.

Two mythical purposes of the tongue have been especially persistent, notwithstanding the fact that it is obviously unfitted for either, and that both can be disproved by a most superficial investigation. The first is that the tongue is used to lick the prey before swallowing. No shape of tongue could be more ill suited to such a purpose than the delicate, almost thread-like tongue of the smaller snakes; yet the myth that snakes cover their prey with saliva to facilitate swallowing has persisted from ancient times down to the present day. I have discussed this belief elsewhere (pp. 657 and 1256).

The other myth—that the tongue of a snake is a stinger, the source of the danger in venomous snakes, is even more fantastic, yet just as indelible. It is a very ancient idea—as evident from Biblical and Shakespearean quotations. But the most surprising thing is that this is one of the most frequently heard beliefs today, as can be verified if one listens to comments by the visitors to the reptile house at any zoo. Let any snake protrude its tongue and someone is sure to exclaim, "Look at it stick out its fangs!", or "Did you see its stinger?"

Slightly more plausible purposes of the tongue have been suggested, and have been a source of argument for many years. Severinus (1651, p. 254) quoted Hodierna as believing that the tongue served the purpose of keeping the animal's nose clean. Charas (1670, p. 41) thought the tongue might be used to catch small creatures; Tyson (1683, p. 44) agreed that flies might be caught in this way. Indeed, Clayton (1693, p. 135) watched a black snake "with wonderful nimbleness" catch insects or flies between the forks of its tongue; and two of my own correspondents claimed to have seen rattlesnakes do this, a quite impossible trick. Allied to this is the idea that the tongue may be employed as a decoy, to attract insects, or even birds, to their destruction. Gosse (1850, p. 151) repeated the statement that the tongue might be used to lap up fluids, although he seemed not to believe this himself.

I have never seen rattlesnakes use the tongue when drinking, even when sucking drops of water from some solid object—a stone, for example—as they sometimes do. Buckland (1859, p. 257) thought the tongue to be concerned with the function of voice—with hissing. Such is not the case, although rattlers, like other snakes, can and do hiss, with or without the simultaneous protrusion of the tongue. Ruskin (1875, p. 185) evidently was so disturbed by the conflicting and fantastic theories that he concluded the busy tongue had no purpose whatever, which may well be considered the most fantastic conclusion of all. Hudson (1893, p. 198) expressed a dual theory as to the purpose of the tongue: Upon the part of a resting snake he thought it a warning device (p. 202); whereas, in the case of a prowling snake, he thought the prey would have its attention so concentrated on the movements of the tongue—a sort of mesmerism—that it would fail to notice the gradual approach of the snake itself, until too late to escape.

In contrast with these supposed physical uses, it was natural that some type of sense reaction should be attributed to the tongue, since anyone watching an exploring snake would be convinced that the flicking tongue must surely be conveying to the creature some impression of its surroundings. Lacépède (1788–89, vol. 2, p. 30; Kerr, 1802, vol. 3, p. 39) thought it an organ of taste, and many others have made the same natural assumption. But Payne (1945, p. 511) states that there are no taste buds in a snake's tongue. Hellmann (1817, p. 7), after one of the most complete investigations up to that date, decided it was used as a feeler—that is, an organ of touch. This interpretation has been concurred in by many later herpetologists, some, of the greatest prominence (e.g., Schlegel, 1837, vol. 1, p. 39; Traill's translation, 1843, p. 52; Duméril and Bibron, 1844, vol. 6, p. 100; Dixon, 1902, p. 992; Boulenger, 1913, p. 74). This was also Miss Hopley's conclusion (1882, p. 124), after her interesting historical survey of the theories that had been then proposed. Occasionally it has been suggested that the tongue is used for sensing air vibrations, that is, an equivalence to an organ of hearing (King, 1941, p. 32; Beck, 1952, p. 141).

All of these theories of the purpose of the tongue have lately been displaced, at least in large part, by the proof, through extensive experiments, that the tongue is an accessory to the sense of smell, in that it serves as a conveyor of external material particles to two pits known as Jacobson's organs in the roof of the mouth. These, in turn, convey to the brain the sensations resulting from the character of the particles. As the sensation-affecting particles are more often secured directly from the air than from contact of the tongue with material objects, it is probable that the tongue should be considered an accessory to the sense of smell rather than taste. However, Jacobson's organs are not the sole source of the snake's olfactory knowledge, for it can likewise detect odors through the nose and the more normal organs of scent.

The new theory of the tongue's use served to solve another problem as well, for Jacobson's organs had also been a puzzle. Boulenger (1913, p. 73) considered them to be probably olfactory in purpose, but thought them operative only during feeding. Eventually the questions as to the purpose of both the tongue and Jacobson's organs, as far as snakes are concerned, were solved by Broman (1920), Baumann (1929), and Kahmann (1932, 1934), who proved the existence of a co-operative relationship involving a combined function. For the tongue serves to pick up

particles or odors in the air; these are then carried into the mouth, the tips of the tongue are introduced into the corresponding pits of the paired Jacobson's organs, which in turn serve to assay the impression thereby received. Baumann showed that European vipers follow both females and prey by this type of chemoreception, and Kahmann (1932) reached the same conclusion regarding the European grass snake (*Natrix natrix*). The external impressions may be conveyed either in the form of material particles that adhere to the tongue or as gases or vapors dissolved in saliva. Further investigations of this mechanism, and its usefulness compared to other organs, both in snakes and lizards, have been made by Noble and Clausen (1936, p. 271), Noble and Kumpf (1936, p. 371), Noble (1937, p. 673), and Bellairs (1942, p. 167). The general conclusion has been that the tongue-Jacobson's organs combination comprises an important olfactory unit, in many species of snakes and some lizards, both with respect to the pursuit of prey and of mates, although it is not the sole olfactory source in any case, nor the most important in many. Wilde (1938, p. 445), working with garter snakes (*Thamnophis*), showed that the tongue-Jacobson's organs combination was important in the feeding reaction of the species tested. However, an actual contact of the tongue or lips with the prey was necessary to stimulate the snake to strike. Bellairs (1942, p. 167) stated that Jacobson's organs reach their maximum development in snakes.

It has long been known that snakes have olfactory bulbs, olfactory nerves, and therefore a sense of smell quite apart from the newly interpreted tongue-Jacobson's organs combination. The tests that have been mentioned as eventually solving the purpose of Jacobson's organs necessitated blocking the response of the olfactory bulbs. Crosby and Humphrey (1939, p. 95) have pointed out the close relationship of these two seats of olfactory stimulation, there being two pairs of olfactory nerves, one, the main olfactory, the other the vomeronasal connecting with Jacobson's organs. They found the accessory olfactory formation (Jacobson's) highly developed in both copperhead and moccasin, from which we may assume that rattlesnakes are similarly equipped.

Observations of rattlers in the field, as well as these theoretical considerations, indicate that rattlesnakes have a keen sense of smell. As I have discussed elsewhere, they have been observed trailing their prey, and they seem able to determine by scent whether a mammal burrow is occupied. As is the case with other venomous snakes, it is their custom to strike their prey, withdraw to avoid any chance of retaliation, and then methodically to seek out the animal, which has usually run a short distance before dying, by following its scent.

Mosauer (1935c, p. 33) believed that the sidewinder hunts its prey by using the tongue-Jacobson's organs mechanism. Cowles (1938, p. 13), who first described the body-blow defensive mechanism by which rattlers defend themselves against king snakes and similar enemies (see p. 1102), found that skunk odor produced the same reaction. Bogert (1941b, p. 331; Stebbins, 1954, p. 335) demonstrated that this defense pattern in rattlesnakes is initiated by odor emanating from the dorsal surfaces of king snakes and other species that are at least in part snake eaters, and that the rattlesnake becomes aware of the danger via the tongue-Jacobson's organs route. Stebbins (1943, p. 128) reported a field observation in which a sidewinder evidently sensed his presence by odor, when the snake reached a point directly to leeward of the observer.

C. B. Perkins makes this interesting comment on the use of the tongue and sense of smell by captive rattlesnakes:

When a cage door is opened, a rattler will assume that it is time to eat, and, if it happens to be the time to clean cages instead, it might strike the shovel used for cleaning and hurt its mouth. If the shovel is moved very slowly close to the head of the snake, to give it a chance to find out what is going to happen, the rattler will test the shovel with its tongue, and then coil up in a corner and pay no further attention to the cleaning.

Superficially, the rattler's tongue does not seem to differ from that of colubrid and other snakes. The base comprises two parallel, conjoined cylinders, distally branching into separate pointed tips. The tips are so thin and delicate that they can hardly be felt when flicked against the hand. Rattlesnake tongues are black at the outer end and flesh-colored inwardly. It is quite easy to stimulate a rattler to extrude the tongue by the slightest disturbance, or by introducing some odorous substance into its cage. The mouth is opened very slightly to permit the egress of the tongue, which is facilitated by a notch in the rostral scale.

A man's reaction, or that of other mammals, indicates that he usually becomes conscious of a new odor in the course of normal breathing, following which he sniffs rapidly to gain a better sense of the stimulus. But snakes breathe much less frequently than mammals, the rapidity depending, not only on bodily activity, but on temperature as well. Their reaction to a new odor never results in sniffing, but on the contrary is followed by a rapid flicking of the tongue. It may be that the inability of a snake's normal breathing to keep the olfactory bulbs in contact with the infrequently inspired air, has led to the development of the easily controlled tongue-Jacobson's organs parallel mechanism.

We may conclude that the rattlesnake's olfactory sense, being innervated by way of two separate and somewhat independent paths, is quite acute, superior, in fact, in importance to every other sense, except possibly sight, with respect to the primary objectives of food, mates, and protection from enemies.

We may inquire whether, of the various theories of the purpose of the tongue that have been proposed, any remain valid, now that its connection with Jacobson's organs and olfaction have been demonstrated. There are, I think, possibly two. The first is as a feeler. Whether a snake touches the objects it is investigating solely to secure particles for transmission to Jacobson's organs, or whether it tests the object in any way by touch may be a subject of some doubt. I rather think the touch itself is of little purpose beyond the possibility of securing particles for examination. One frequently sees an exploring snake with flicking tongue, making no effort to touch anything, the air-borne particles being sufficient for its purpose.

But as to one other purpose, that of an action calculated to alarm an enemy, a much better argument can be advanced, with a particular applicability to rattlesnakes. The extent to which it is evident among other crotalids I have not investigated. A rattlesnake that has been alerted by some movement, odor, or tremor of the ground, responds by flicking its tongue in and out repeatedly and rapidly. While the tongue is out it will be seen to pass quickly through a considerable vertical arc. If the snake be further alarmed, it then throws itself into its striking coil; its mien changes completely, for now it threatens by rattling and hissing, while the head is drawn back like a poised javelin. And simultaneously the use of the tongue changes. There are now much longer intervals during which the tongue

is extruded to its limit and much shorter intervals of withdrawal. Not only is the outward extension greater than when bent solely on investigation, but the quivering tips are more widely separated, and the tongue is first pointed vertically downward and then erected vertically with considerable pauses in each position (fig. 7:2). Sometimes it will change from one to the other of these opposite positions several times before withdrawal. Often the extrusion is so great that the tongue cannot be held exactly erect but falls off slightly to one side. But it does not seem possible that this handling of the tongue can apprise a snake of the nature of an intruder any better, if indeed as well, as the more rapid flicking. That it adds to the snake's pugnacious appearance there can be no doubt, and I am therefore of the opinion that it is a part of the threatening posture designed to frighten an enemy. It certainly does add to the spine-tingling picture.

### THE FACIAL PITS

The pit vipers comprise a family of venomous snakes, the Crotalidae—by some herpetologists considered a subfamily, the Crotalinae—characterized by, and called pit vipers because of the presence of a deep pit, or facial opening, on each side of the head.<sup>27</sup> In the rattlesnakes, the pit lies somewhat below a line from the nostril to the eye and slightly nearer the former (figs. 2:68 and 2:69). It is larger and more conspicuous than the nostril. Because of its location in the position occupied by the loreal scale in snakes without pits, the organ is often referred to as the loreal pit. It is externally quite evident as an opening neatly lined with scales, and with its axis pointing forward, rather than perpendicular to the surface of the head. The fundamental importance of the pit (including a cavity in the maxillary bone to accommodate it), both as an organ and as an indicator of relationships, has long been appreciated, as is shown by the use of its presence or absence to distinguish two widespread groups of snakes that otherwise bear such obvious structural similarities as do the Viperidae and Crotalidae. The Viperidae—the pitless vipers—are found only in the Old World, in Europe, Asia, and Africa; whereas the Crotalidae range throughout most of Asia (with a single species entering southeastern European Russia) and also throughout much of North and South America. Representatives of both families occur in the Indo-Australian Archipelago, but not in Australia itself. The rattlesnakes, occurring only in the Americas, comprise one subdivision of the pit vipers.

Since the earliest days there have been many theories as to the purpose of the pits. Their location on the sides of the head naturally led to the supposition that they comprise some kind of a sense organ. Tyson (1683, pp. 26, 51, 57) thought possibly they were ears, although the lack of an inner opening led him to question this conclusion. He recognized the fact that European vipers are without these organs. Lawson (1709, p. 129) believed them to be extra nostrils, a supposition repeated by Brickell (1737, p. 145) and retained, by implication, in Latin America, where the name *cuatro narices* (four nostrils) is still widely used for pit vipers. Clavigero (1937, p. 389, but writing in 1789) thought the pits were ears, as did Lacépède (1788–89, vol. 2, p. 122; Kerr, 1802, vol. 3, p. 318), when he noted them in the fer-de-lance. Home (1804, p. 72; see also Russell, 1804, p. 70), from a careful anatomical examination, concluded that the organs could not be ears; he reached

<sup>27</sup> Higgins (1873, p. 88) is the only author known to me who misunderstood the meaning of the term; he stated that pit vipers received the name through their frequenting pits or caves.

no final conclusion as to their purpose, but thought they might be analogous to the tear sacs of certain ruminants, serving to wash the cornea. Desmoulins (1824, p. 264), who made one of the most thorough early investigations of the pit structure, thought they were olfactory in purpose. Harlan (1835, p. 501) believed they might serve to bring air into contact with the venom, thus affecting its chemical properties. Schlegel (1837, vol. 1, p. 57; Traill's translation, 1843, p. 67) thought them accessory to the nose, that is, an organ of smell. R. Owen (1866, p. 555) referred to them as secretory follicles having an unstated purpose. Leydig (1868, p. 89; 1872, p. 317; see also Hoffmann, 1894, vol. 3, p. 1410) considered them the organs of a sixth sense, unspecified in character. West (1900, p. 49) thought them possibly similar in function to the lateral-line sense organs of fishes, which detect pressure variations in the water, and, through reflected waves, the presence of near-by objects. Chabanaud (1924, p. 453) considered them as being tactile in function.

Lynn (1931, p. 97) made a very careful and complete anatomical investigation of the pit and its accessory nerves. He concluded that, as the pit has no direct connection with any other organ of the head, either by means of a duct or other opening, it can be neither a nasal opening leading to the olfactory organ, nor an auditory opening connected with the ear (p. 124). He also disproved any secretory function (p. 125). From the structure of the pit he concluded that it should respond to a certain type of tactile stimulus, namely, air vibrations (p. 133).

Noble, who, with Arthur Schmidt, eventually supplied the currently accepted theory of the pit, first announced in 1930 (p. 477) that the pit responded to air disturbances produced by a passing enemy or prey, serving both to arouse the snake and to enable it to strike with greater accuracy. This theory was elaborated in a paper read in 1934, only a summary of which was ever published (Noble, 1934, p. 4). Finally, Noble and Schmidt (1937, p. 263) announced the theory that the pit is a temperature-differential receptor, by which the snake is enabled to determine the direction of objects having higher temperatures than their surroundings, of which a warm-blooded creature such as a bird or mammal would be a good example. Thus the pit aids both in locating prey and striking it. Noble and Schmidt proved this theory by experiments with snakes having all other senses destroyed or blocked off. For targets they used incandescent lamps covered with black paper, whereby the heat could be readily controlled. They found that snakes, with only the pits available as sense organs, were able to, and would, strike quite accurately at the covered lamps while heated, but lost their ability to detect them when they cooled. They found the snakes able to locate a moving, heated lamp at a distance such that it produced a temperature only  $0.2^{\circ}\text{C}$ . ( $0.36^{\circ}\text{F}$ .) above the surrounding air at the pit (see also Ruth C. Noble, 1945, p. 6). With objects having a surface temperature of  $69^{\circ}\text{C}$ . ( $156.2^{\circ}\text{F}$ .), with a room temperature of  $26.4^{\circ}\text{C}$ . ( $79.5^{\circ}\text{F}$ .), Noble and Schmidt determined the recognition distance to be about 250 mm. (10 in.). The maximum recognition distance was 350 mm. (13.8 in.). But this was with an object having a surface temperature higher than that of any prey. From these experiments, it appeared that the thermoreceptive function of the pit is essentially of short-range value. It should have a somewhat greater range at lower air temperatures than higher, since the detectable temperature differential produced by the warm-blooded prey would be experienced at a greater distance.

and should therefore be particularly useful at night. C. M. Bogert has called my attention to the fact that the strike was the only recognition indicator accepted by Noble and Schmidt; he believes actual recognition of the warm object, as might be first indicated by a flicking tongue, may prove the pit to have a greater range than the Noble-Schmidt experiments suggest. This has, indeed, been demonstrated by the later experiments of Bullock and Cowles (1952, p. 541).

Noble's original idea, that the snake was able to sense air movements by means of the pit, was not eliminated by the new theory; rather, this was relegated to a secondary and less-important function. Bullock and Cowles (p. 542) subsequently concluded from their experiments that the detection of air movements has little importance with respect to the function of the pit.

The Noble-Schmidt experiments were performed, not only on pit vipers, but also on several snakes of the boa-python group that possess a series of small pits on their lips. The tests showed these to have the same thermoreceptive functions as the larger and more prominent facial or loreal pits of the crotalids; indeed, tests on a python by Ros (1935, p. 1) were the first to indicate that the ophidian labial pits might be radiation receptors. Although appropriate experiments have not yet been made, the guess has been hazarded that certain small supranasal cavities found in several genera of Old World vipers—*Bitis*, *Pseudocerastes*, and *Eristocophis*—may serve the same purpose. These have been discussed by Boulenger (1893-96, vol. 3, p. 493), K. P. Schmidt (1930, p. 228), Parker (1932, p. 222), Noble and A. Schmidt (1937, p. 285), and Malcolm Smith (1943, p. 19).

The most important recent work on the function and mode of operation of the facial pit has been that of Bullock and Cowles (1952, p. 541; see also Everest, 1953, p. 125). Using curarized rattlesnakes of several species, they cut one of the three nerves ramifying into the pit membrane and ascertained the nerve responses to various stimuli. The tiny nerve currents were amplified to give clear quantitative indications of the degree of stimulation. The experimenters found no response to sound, odors, vibration of the substratum, touching the head or pit, or heat-filtered light of moderate intensity. Mechanical deformation of the pit diaphragm by an exterior instrument, or by a puff of air, did produce a moderate effect.

But the nerve showed outstanding sensitivity to radiant heat impinging on the diaphragm. Any warm or cold object elicited a response, as, for example, a human hand at 300 mm. (11.8 in.), or a glass of water at a temperature 1° C. (1.8° F.) above or below that of another glass placed to set a neutral temperature level at the pit. The neutral level was found to depend on the average radiation of all objects in the field of reception; this neutral level was determined to be independent of the snake's own body temperature.

Thus it was shown that the pit serves to recognize the presence of any object that is warmer or colder than its surroundings or the other objects that set the temperature level in the field of reception. This field was determined to include a cone extending horizontally from 10° across the midline to a point approximately at right angles to the snake's body; and from 45° above to 35° below the horizontal. These experiments prove that the pit is a radiation receptor that can alert rattlesnakes to the presence and direction of objects slightly higher or lower in temperature than the general surroundings, and through its stereoscopic nature, is an important adjunct to securing prey and self-protection.

It is interesting to record that R. W. Jones, as early as 1892 (p. 277), observed that a lighted match held in front of a timber rattlesnake (*C. h. horridus*) seemed to anger it more than anything else. No doubt it was the pit rather than the eye that caused this reaction. Kunzé (1879, p. 311) observed that a rattlesnake, partly blinded by incipient shedding, could strike a mouse as accurately as when the eyes were not dimmed.

The earliest anatomical investigations of the pit were those of Tyson (1683, p. 25), Home (1804, p. 72), Desmoulins (1824, p. 264), and West (1900, p. 49). Home is to be credited with the discovery of an inner compartment in the pit; Desmoulins first noted its heavy nerve supply; and West observed that the nerve terminations are concentrated in the diaphragm between compartments.

The most complete descriptions of the pit structure are those of Lynn (1931), and Noble and Schmidt (1937). The pit is really dual (Lynn, fig. 3, p. 105), comprising an anterior section which is the part so clearly evident externally; and, hidden behind a separating diaphragm, an inner, posterior compartment of smaller size. The latter is also open to the atmosphere, but only by way of a narrow entrance—virtually a pore—that is hidden under the posterior bottom edge of the lower preocular scale, the crescent-shaped scale below the large scale directly in front of the eye. The location of the pore was first pointed out to me by Charles E. Shaw. It is not to be confused with the large irregular cavity in front of the eye: it does not open into this cavity but is anterior to it. According to Lynn (1931, p. 105) the opening is surrounded by a sphincter muscle whereby it may be opened or closed.

From this orifice a narrow canal leads into the inner compartment of the pit, serving to equalize the air pressure on the two sides of the diaphragm. Thus radiant energy impinges only on one side of the diaphragm; and, as air is admitted to both sides, hence equalizing the heat of convection, any temperature difference must be the result of radiant heat impinging on the outer face of the membrane.

Block (1950, p. 284) suggested that the pit operated as a pneumatic radiant-energy detector of the Golay type, functioning through deflections of the pit membrane or diaphragm, but the experiments of Bullock and Cowles would seem to disprove this, for they cut the diaphragm and found no resulting loss of response.

The cells lining both the inner and outer chambers of the pit are ectodermal in origin; when the snake changes its external skin the cavities can be distinguished as bags attached to the shed skin. The fact that the shed skin of the inner cavity can be withdrawn through the narrow entrance that seems hardly larger than a pore, indicates that this entrance can be dilated when necessary.

According to Lynn (1931, p. 132) the pit membrane is richly supplied with nerves derived from the ophthalmic and supramaxillary branches of the fifth cranial nerve, which serve to transmit to the brain the effects of the radiant energy impinging on the nerve termini located in the diaphragm. The nerve used by Bullock and Cowles in their experiments (1952, p. 541) was the superficial branch of the superior maxillary division of the trigeminal nerve branching from the fifth cranial; this is one of the three nerves ramifying in the pit diaphragm. The inner chamber of the pit is bedded in a hollow of the maxillary, a cavity characteristic of the crotalids.

Ontogenetic studies indicate that the pit was evolved by the partial fusion of

two pits of the same type as the labial pits of the present boids (Noble and Schmidt, 1937, p. 283). But the crotaline type is an improvement over the more primitive boid form since, by reason of the diaphragm, nonradiant effects may be eliminated. Noble and Schmidt (1937, p. 286) report that crotalids are less mechanical in striking at warm objects than the boids. They also observed that the odor of prey caused tongue movements, whereas a temperature differential brought on a strike.

The pit membrane is so thin as to be translucent. It is slightly pigmented in some of the darker rattlesnakes—the southern Pacific (*C. v. helleri*), for example. Whether the nerve termini on the front surface are darkened, as might be expected in a radiation receptor, has not been made clear by those who have studied its histology.

As one looks into the pit of a live rattlesnake from the front, with the membrane under intense illumination, a groove will be noted across its face. This groove is almost vertical but with the lower end diverging outward. Occasionally, if one uses the groove as a point of reference in line with an outer edge of the pit, some movement in the membrane or possibly the direction of the opening seems evident. I am of the opinion that there is a movement produced by muscles that are evident as a swelling which begins at the lip—the supralabial scales—and extends upward to a point behind the pit. This bulge seems more prominent in an aroused snake; it may serve to dilate the pit and even slightly to modify the direction of its axis.

#### TOUCH

Since snakes have no tactile appendages such as legs, the sense of touch is not so important to them as it is to many other kinds of animals. Yet, despite their being sheathed with scales that might be expected to dull their sensitivity, they are apparently responsive to the slightest external contact. I have already mentioned their susceptibility to ground tremors, allied as this is to hearing (p. 394). Similarly, the tongue may occasionally be used as a tactile organ, although this is not its most essential use. The chin, also, may be so employed; this is definitely the case in snakes of some genera.

Dropping particles of sand on rattlers or brushing them with feathers show them to be sensitive even to these light contacts; if not sufficiently aroused to coil they will at least indicate attention by flicking out the tongue to discover the source of the annoyance.

It has been reported that rattlers exhibit a pleasurable response to petting. Crèvecoeur (1782, p. 348; Bingley, 1803, vol. 3, p. 75; T. Smith, vol. 6, p. 94) tells of a tame rattlesnake that so enjoyed being stroked with a brush that it would roll on its back like a cat. This story is to be deemed on a par with Crèvecoeur's other famous folklore item—the fatal boot (p. 1281). The late Mrs. Grace O. Wiley (1929, p. 13) had a western diamond (*C. atrox*) so tame that it would arch its back when stroked with her hand, although it did not respond in this way to other people. Another western diamond, although quite tame, never arched its back when she stroked it. Both were males. I think it should be said that the petting to which one of the rattlers reacted was not the cause of its pacification, as one might expect in a dog; on the contrary, the reaction was evident only after the snake had been tamed. Mrs. Wiley also reported (1930, p. 100) that gentle stroking aided in

handling specimens of the Mexican west-coast rattlesnake (*C. b. basiliscus*). Her fearless handling of venomous snakes was well known to her contemporaries, yet even she had to exercise the greatest patience, involving no little danger, to achieve the results for which she became famous. And even in her case, after many years of experience, there was a fatal termination. No ambitious amateur should ever presume that petting is sufficiently soothing to render a strange rattlesnake safe for handling.

#### DISTANT DETECTION

It is a common experience in the field to have a rattler suddenly sound off when the observer is still at some distance. The sense by which the snake has become aware of the intruder is generally difficult to determine. One would first suspect sight, yet it often happens in these cases that there are intervening objects. Since rattlesnakes are deaf to air-borne vibrations, as every evidence indicates they are, then either ground tremors, or the sense of smell is the avenue of perception that serves to warn the snake. I deem the pit of too short a range to be useful in such a situation. Some typical cases of distant detection, as described by my correspondents, are the following:

On one of my hunting trips, I found a rattler that I heard buzzing when I was at least 65 feet away. I do not know how the rattler discerned my presence. It happened to be on a heavily wooded hillside and there was very little or no undergrowth. *Harry Z. Cole, Norristown, Pa.*



Most rattlers I have found remain very still when first discovered, or try to get away. When they are molested they immediately coil in a position to strike and begin to rattle. One morning I heard one start to rattle before I reached it. I measured the distance to it, which was 132 feet. *Herbert P. Rice, U. S. Forest Service, Meadville, Miss.*



I have known a rattler to show activity when an approaching person was still 200 feet away; yet, others—maybe asleep—did not move until touched with a stick. *John C. McNelly, Prescott, Ariz.*



There has always been a question in my mind as to whether rattlesnakes hear or see, because I have observed large diamondbacks at times when they would raise their heads and rattle when I was as far as 100 feet away; and, as I came closer they would have their heads turned away from me but they kept on rattling. *Jess T. Fears, U. S. Forest Service, Payson, Ariz.*



When riding horseback, I have heard rattlers sound off at least 100 yards before I got to them. *C. K. Lyman, Newport, Wash.*



A Pacific rattler was disturbed and commenced to rattle prodigiously while I was still 150 feet distant and long before I discovered him. From our relative positions, it seemed almost impossible that he could have seen me. *Brighton C. Cain, Oakland, Calif.*



I was riding a horse along the Santa Ynez River bed when I heard a snake buzzing while I was still some 200 feet from it. I rode on and finally spotted it about 20 feet off to one side of the trail in an open place near some thinly set willows. The snake was coiled and had its head raised 8 or 9 inches above the coils, and was very much on the fight. On account of the shrubbery, the rattler could not have seen my horse until I got within 40 feet of it. I did not see signs of anything else that might have disturbed it before I got there. It is my opinion that the snake felt the vibration caused by the horse traveling rather than by seeing or hearing it. *Walter F. Emerick, Division of Fish and Game, Palmdale, Calif.*

I was riding a trail on the Eel River in Lake County and heard a snake rattling on a ridge, about 200 feet away. When I got over there he was coiled up and rattling as loud as he could. *M. W. Durham, U. S. Forest Service, Pasadena, Calif.*



In late July or early August of 1938, a companion and I were hiking up a hillside in the afternoon. Up the trail we heard a rattler suddenly burst forth with its warning rattle about 30 feet in front of us and about the same distance to the right of the trail. We couldn't see it as the area was rather well covered with a growth of deerweed. We started toward the spot from which the noise came and finally discovered a southwestern speckled rattler (*C. m. pyrrhus*) about 3½ feet long lying under a large sumac bush. I don't know why the snake ever rattled in the first place, as it was well away from us, and so well concealed by intervening brush that we would have never noticed it had it not advertised its presence. From its location, I don't think it was possible for it to see us. *Charles E. Shaw, San Diego, Calif.*

Through the years, I have, myself, had similar experiences with a variety of species of rattlesnakes—with southern Pacifics, red diamonds, speckled, and tiger rattlesnakes. In one instance a snake rattled violently in a thick sumac bush 100 or more feet from where we were hunting. In another, Dr. E. H. Taylor and I were walking down a creek in Doane Valley on Palomar Mountain. The erosion had made deep cuts so that the banks were high above us on either side. A southern Pacific rattler on a grassy shelf on the bank above us rattled as we passed below. It was found to have bluish eye coverings, preparatory to skin changing. Since we were hidden from it, it must have sensed our presence by vibration or odor.

Similar accounts have been published by Williston (1878, p. 203), J. D. Mitchell (1903, p. 36), and Linsdale (1932, p. 383).

Linsley (1843, p. 44) reported that a rattlesnake in a barrel could detect a man's approach, although he walked in stocking feet; and Reichert (1930, p. 262) noted that a western diamond in captivity was able to detect him, even though behind a door, at a distance of some 12 feet. However, the nature of the floors involved are not mentioned; they may have been such as to transmit a tremor.

Charles M. Bogert, of the American Museum of Natural History, has this to say about the senses of rattlers:

Pondering the questions you raised concerning the senses of rattlers, I was reminded of our experiences when Dr. Cowles and I were camped near Indian Wells. Time after time we'd see no evidence of rattlers near camp; then we'd walk around a patch of mesquite, about a city block in size—mesquite blocked off by roads—and return to camp to find that one or more rattlers had crossed the road that could be kept under observation from camp. We were inclined to believe that *atrox* was a pretty cagey snake, on the *qui vive* through one sense or another. Did they see us, hear us, or merely catch vibrations through the ground? We were convinced that they knew somehow when the coast was clear.

Thus, from these many experiences, we are certain that, whatever the limitations and imperfections of a rattlesnake's senses, their cumulative value is such as to serve well in advising them of the approach of danger, at least in the form of a creature as large as a man. It will be noted, in the cases of the field notes sent me by correspondents, that men on horseback were usually detected at greater distances than those afoot. This, it seems to me, seems to support the ground-tremor theory of detection. Tschiffely (1933, p. 214) saw few snakes on his long horseback ride through the Americas; he thought the tread of the horse might have warned

them out of his path. Hudson (1919, p. 18) reported it difficult to catch vipers in England if one trod heavily while searching for them. Rose (1950, p. 217) thinks the danger from mambas in Africa is increased because, being often in trees, they receive no distant ground-vibration warnings of the approach of men, and hence are come upon suddenly.

#### AGGREGATION AND SEX RECOGNITION

Without doubt it is the rattlesnake's acute sense of smell that enables it to follow its fellows—the leaders must have some homing instinct—to a general gathering place for winter hibernation, and to find a mate in the spring. But, with respect to the source of the odor that is trailed, there remains some uncertainty. There appear to be family differences, and the rattlesnakes have not been adequately investigated to determine the facts respecting this group.

Baumann (1929, p. 36) found that the male European asp (*Vipera aspis*) probably followed the females as a result of discharges from the anal scent glands. Noble and Clausen (1936, p. 303) showed that, with De Kay's snake (*Storeria dekayi*), vision is the primary sense used in aggregation; while sex recognition is through some odorous substance contained in the dorsal skin. Noble (1927, p. 695) proved that sex recognition in the garter snakes (*Thamnophis*) also has its seat in odorous skin substances, rather than in the anal scent glands. Whether this is true of the rattlesnakes is not known. One should expect some sex reaction to the postanal gland discharges since the female glands are larger than the male. The use of the glands in defense is discussed elsewhere (p. 473). Courting male rattlesnakes use the tongue actively in a characteristic manner. It is flicked out at intervals of a second or less; sometimes it is seen to touch the body of the female, but not always. This tonguing is accompanied by jerky, questing movements of the head.

Woodbury, in his studies of the Great Basin rattler (*C. v. lutosus*), was convinced that as soon as a few rattlers had entered the traps set at dens, they served as a lure for others to follow.

#### INTELLIGENCE

Although no snakes have the degree of intelligence with which the myths of bygone days would credit them—the wily serpent aura—they do, of course, have enough intelligence—if that is the proper word for a creature of such reduced mental capacity—to satisfy the needs of food, self-protection, and reproduction, and thus to survive. The degree of intelligence that a snake exercises can be judged only when it is alert in fulfilling one of these primary motivations, for at other times it seems so dull as to be almost comatose. Because they are more active, the slimmer kinds of snakes have an appearance of being more alert than slower, heavier kinds like rattlers; but whether they are more intelligent we cannot be sure. There are some indications that the cobras are more sagacious than most snakes.

A rattler accustomed to feed in captivity shows, upon the approach of its keeper, an alert attentiveness that gives one a sense of intelligence. The lively way in which it rises up and faces the door of its cage when it is opened, the recognition of its regular attendant or his routine, the ability to distinguish a food forceps from a cleaning shovel, all testify to an appreciation of procedures. The observations of Tevis (1943) and Fitch (1948) show similar discriminatory actions upon

the part of a hunting rattlesnake in the field—actions not of purely stereotyped patterns, but fitted to the needs of the occasion.

Similarly, a rattlesnake discovered in the wild seems to exercise some acumen in determining when to abandon passive concealment in favor of flight, and when to turn and endeavor to intimidate an enemy. Rattlers are often found basking in front of holes or crevices that will furnish a refuge in emergency, another indication of a primitive astuteness. They know well how to threaten, and at the same time to retreat toward some place of safety.

That rattlesnakes come eventually to know their keepers, there can be no question. Gowanloch (1913, p. 56) tells of a canebrake rattler (*C. h. atricaudatus*) that recognized people and would only rattle at a stranger. I saw, in one collection, a western diamond that showed no fear of handling by his owner but adopted a defensive attitude when I came near. But, without doubt, the most informative experiments were those of Mrs. Grace O. Wiley (1929, p. 8; 1930, p. 100), who kept a number of rattlers of different species as pets. They manifested their recognition of her in various ways, particularly in an absence of fear.

Stanley (1897, p. 29), a veteran of the snake-oil circuit, stated that it was his practice to allow his rattlers to smell his coat to reassure them before he handled them. Matteson (1899, p. 665) reported that rattlers are quick to sense fear upon the part of an intruder. One may presume that, to whatever extent this idea is justified, it probably results from the rattler's becoming alarmed at the quick movements made by a frightened person.

This naturally brings up the question of whether rattlesnakes can be tamed. The answer is that they can, as has been demonstrated by Mrs. Wiley and many others. This is not at all surprising, for rattlers are not inherently vindictive or vicious. Like all wild animals they are fearful of unaccustomed situations and wary of strange creatures, toward which they adopt defensive tactics that appear to us to be violently aggressive. To whatever extent they can be cured of fear, they may be considered tame—that is, they will not bite—but there is always the danger of a sudden fright, and no one should handle a supposedly tame rattler.

As early as 1615, Hernández (fol. 192<sup>v</sup>; 1628, p. 330; Nieremberg, 1635, p. 269; Jonstonus, 1653, p. 27) stated that the Indians tamed rattlesnakes by wrapping them with fine linen—just how this was done is not made clear. Crèvecoeur (1782, p. 248) and other writers of colonial days mention tamed rattlers, always gilding the stories with tales of their coming when called. The fact remains that many rattlers, when they have become accustomed to people and their surroundings, will offer no objection to gentle handling, and to that extent may be called tame. Of course, there are both species and individual differences. Some species are more nervous than others. Davenport (1913, p. 120) says that only one western diamond (*C. atrox*) out of 100 can be made a pet. Although it is true that this is a notably highstrung species, I should not consider amenable specimens nearly so rare. There are individual differences within each species. Some become quickly accustomed to people, while others will rattle at the approach, even of a keeper, after years in captivity. Tamable or untamable, I hope nothing I have said will suggest to anyone that tame rattlesnakes are really safe to handle. One can visualize a dozen kinds of slips or accidents that might occur, while holding a tame snake, that would frighten it into biting. Only scientific and controlled investigations for a

definite purpose can ever justify what would otherwise be a foolhardy and unnecessary risk. The experiences of countless snake handlers have shown that no snake is ever tame in the sense that it will not bite if accidentally frightened or injured.

Embroidered and fantastic stories of rattlesnake intelligence are not lacking. Some of these are really believed by their authors, while others are humorous campfire exaggerations taken too seriously by some tenderfoot. They are treated more fully under the head of myths (p. 1256), but a few may be mentioned to indicate the type.

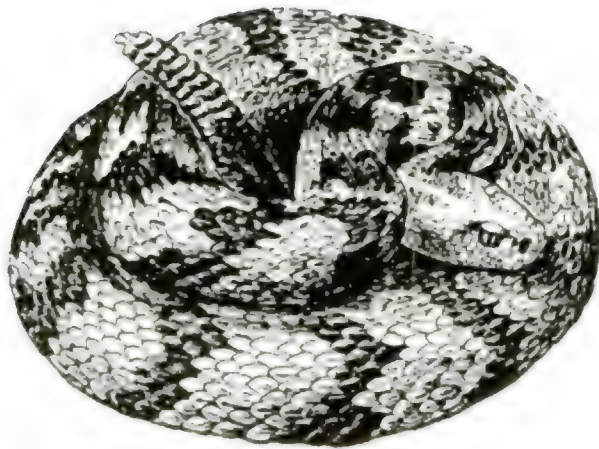
Wildwood (1862, p. 227) tells us of the man, who, while hiding from the Indians, found himself lying beside a big rattler. He played dead, and the snake, after satisfying itself of his demise, crawled away.<sup>28</sup> Thus we have the rattlesnake replacing the lion of a familiar African tale. Behind this there is the sensible advice to remain immovable if one finds himself within striking distance of a rattlesnake in its striking coil, at least until the situation has been surveyed to see which way to jump. Anyone close to an outstretched rattler or one in its resting—pancake—coil can easily step out of the danger zone to safety without being particularly concerned.

Benton (1915, p. 80) tells us of a rattler that had the run of its master's cabin. Upon the advent of a stranger it was told to "git in yore bed" which it promptly proceeded to do.

Brown (1936, p. 24) tells how the rattler defeats the machinations of the wily prairie dog that would entomb him. When he goes down a prairie-dog hole he proceeds but a short distance and then turns about, facing the entrance. Then if the dogs start to pile earth into the hole to bury their ancient enemy the rattler will come out at once. The author claimed to have tested this by dropping a little earth down a hole; he found it the most efficient way to cause a rattler to emerge. But C. B. Perkins reports that a rattler at the entrance of a prairie-dog hole will escape down the hole if disturbed, whether by bits of earth or otherwise.

Meek (1946) relates a number of interesting but impossible yarns of the intelligence of the diamondback. One, observing (p. 12) from the edge of a large field that a rough spot in the center, where it was accustomed to hunt, had been cleared, turned back into the woods. Another (p. 83) used a drain pipe regularly to cross a sandy road, in order to avoid making a track where it could be seen. One wise diamondback had no difficulty in selecting, for attack, from a ring of men surrounding it, the particular individual who had traitorously divulged its hiding place to the others.

<sup>28</sup> Wildwood says this happened to one John Lewis. A similar story is to be found in the *Common-Place Book* of Margaret Lewis written about 1780, her son Charles being the threatened victim (see Margaret L. Lewis, 1892, p. 210).



## 7. Behavior

### TEMPORAL ACTIVITY AND LIMITATIONS

In their habits, rattlesnakes, like all reptiles, are strongly affected by the temperatures of their surroundings. They lack any internal means of controlling to a material degree, either the level, or the range of variation, of their body temperatures. The several physiological devices for temperature control or amelioration possessed by the so-called warm-blooded creatures, the mammals and birds, are absent in reptiles. With some exceptions, birds and mammals have various mechanisms for maintaining their internal temperatures at a fairly constant level, one that is most suitable for the maintenance of their bodily activities. This constancy of temperature at an optimum level is achieved by the speeding up of metabolism—the development of internal heat by chemical processes—whenever the outward flow of heat through radiation or conduction would otherwise cause a fall of internal temperature to a suboptimum level; or by artificial cooling through increased evaporation from external or internal surfaces, or by internal ventilation (in birds), when external temperatures or muscular activity would otherwise produce a supraoptimum internal temperature. Reptiles, including rattlesnakes, with none of these methods of either achieving or controlling internal temperatures, at least to any important extent, are subject to the vagaries of their surroundings; as the temperature falls the body temperature correspondingly drops, and a point is reached when muscular activity is no longer possible and the animals are completely helpless; or, in the other direction, as air and ground temperatures rise, at a level that would hardly inconvenience most mammals, the reptilian blood, nerves, and muscles are so adversely affected by heat that the animal quickly dies. To mitigate the effects of these deficiencies in their internal control of body temperatures, reptiles instinctively take advantage of temperature differences in their surroundings, by such simple expedients as seeking refuge down holes when the surface temperatures are too high, or by basking in the sun when ground or subterranean temperatures are low.

That snakes may deviate slightly from the temperatures incident to their surroundings has long been known. Extensive studies on such deviations were made by Benedict (1932). Lueh (1941a, p. 126) made experiments on garter snakes

(*Thamnophis*) and water snakes (*Natrix*), and found them apparently able to raise their body temperatures, under particular circumstances, by as much as 5° C. (9° F.), through metabolism when they were cold; and to reduce their temperatures (when external conditions produced uncomfortable heating) by as much as 1° C. (1.8° F.) through evaporation. That these deviations could be maintained for any length of time is doubtful. Furthermore, metabolism becomes inoperative at extreme low temperatures when its heat production becomes most necessary. In any case, it will be noted how minor are the deviations from the temperatures of the surroundings, compared with those normal to mammals and birds.

The warm-blooded creatures—the birds and mammals—are usually referred to as homoiotherms (having constant temperatures), while the cold-bloods, such as the reptiles, are called poikilotherms (having variable temperatures). Cowles (1940, p. 549) prefers the terms endotherms and ectotherms, as being more indicative of the essential difference between the two groups, the terms referring to the source of heat, whether internal or external, rather than to constancy versus variability in the resultant temperature.

Some early writers attributed the inability of reptiles to withstand low temperatures to their lack of such protective or insulating coverings as fur or feathers. This is reasoning backward. For a creature whose body temperature is largely dependent on its own metabolism, and which, by internal control, holds that temperature constantly at an optimum, any divergence impelled by external temperatures is generally adverse, and therefore it is to the advantage of the endothermic animal to have an insulating covering. True, there are some conditions—such as that which exists when muscular activity is high and the heat gradient is outward—when the covering is disadvantageous<sup>1</sup>; but in most situations under which birds and mammals live, their feathers and fur are beneficial, and, in the colder climates, absolutely essential. Without these coverings the energy loss would be so great that no practicable feeding schedule could meet it.

But the reptiles, securing their heat from without, are best served by skins that

<sup>1</sup> Martin (1930, p. 561) points out that man, because of his nakedness and large area of skin with sweat-glands, is the best adapted of all creatures to withstand high external temperatures. The astonishing exterior-temperature tolerance of human beings for short periods has been shown by tests conducted by Blockley and Taylor (1919, p. 111) on men who endured air temperatures up to 240° F. (115.6° C.) for 20 minutes, and 140° F. (60° C.) for over 60 minutes. The importance of temperatures in the normal life of man has been outlined by Mills (1949, p. 267), and the amelioration of adverse conditions by the scientific selection and use of clothing by Siple (1944, p. 412) and Wulsin (1953, p. 105). Phillips (1948, p. 331) has shown that birds can withstand temperatures of the external air that would be quickly fatal to a rattlesnake. The nature and beneficial effects of the cooling mechanisms (and warming as well) that give the warm-blooded creatures such a superiority with respect to internal temperature control, are set forth by Rodbard (1948, p. 418; 1953, p. 137). With these protective devices and the control that governs them, the warm-bloods, in the interests of metabolic efficiency, are able to skirt closely but safely below dangerous internal temperatures. Their physiological elements have evolved in the direction of higher temperatures, whereas the reptiles, dependent on exterior impinging temperatures, have retained muscle, nerves, cell structure, and blood best suited to the average internal temperatures resulting from the external heat flux. As a result, some mammals and birds now have normal internal temperatures that would be fatal to a snake. Rodbard (1953, p. 140) has pointed out that the reptiles have thermosensitive brain centers that affect blood pressure and other functions, but with results on body temperature that are virtually negligible, since they lack the physiological heat absorbing and dissipating mechanisms that are so important to the birds and mammals. According to Heilbrunn *et al.* (1916, p. 404; Heilbrunn, 1954, p. 70) animal cell structures differ in heat resistance to such an extent that temperatures endurable by one species might be quickly fatal to another. Cells destroyed by heat become lethal poisons in themselves.

interpose the least barrier to heat transfer. There are, of course, some conditions wherein insulation would be beneficial—when the temperature is falling below the optimum and the animal might profit from stored heat, for example—but, by and large, the lack of insulation is advantageous. This is the reason why most reptiles, especially snakes, feel cold to the touch, for they are usually at a temperature well below that of the human hand, and are good conductors of heat.

The same considerations may have resulted in the greater average attenuation in body shape of the ectotherms compared with the endotherms—that is, their higher ratio of surface to bulk. For, although the reptiles are penalized by the lack of heat storage when exterior temperatures are falling below the optimum, they profit through rapid and more uniform heating when the conditions are reversed. Basking is particularly effective in the case of an attenuated creature.

Since rattlesnakes, like other reptiles, are fundamentally dependent, for muscular activity and the processes of digestion and gestation, on external heating rather than on the chemical heating derived from their own metabolism, it follows that they can live only in places where the daily and seasonal persistence of adequate temperatures is of sufficient duration to permit the successful completion of these processes. Thus it is that reptiles are so considerably limited to tropical and temperate zones, and even there, at the colder limits, they have been forced to a two-year reproductive cycle, for the young cannot be brought to term in one.

With creatures so dependent on external conditions, it is natural that the activities of rattlesnakes should be greatly influenced by the temperatures of their surroundings, including the radiant heat from the sun, and so we find that their seasonal and daily habits are strongly affected by thermal conditions. Since suitable temperature ranges are met at different times of day and in different seasons, in the various latitudes and longitudes inhabited by rattlers, we naturally find notable habit differences within a single species. Of course, any rattlesnake activity is the result of some phase of the primary rattlesnake objectives, which are food, reproduction, and self-preservation, and their habits must be so arranged as to fit the pursuit of these objectives into zones of permissible temperatures. No generalities with regard to the seasonal or daily activities of rattlesnakes are valid without our taking temperature into consideration.

Cowles and Bogert (1944, p. 277), discussing limiting temperatures and thermal zones to which desert reptiles respond in specific ways, list the following levels: (1) the lethal minimum; (2) the critical minimum; (3) the voluntary minimum; (4) the basking range; (5) the normal activity range; (6) the maximum voluntary tolerance; (7) the critical maximum; and (8) the lethal maximum. Actual figures translating these levels into body temperatures are largely unavailable for rattlers. Air temperatures at which certain responses have been observed are not so important as might be presumed, since they seldom represent the actual body temperatures being experienced by the rattlesnakes; for body temperatures are the resultant of all thermal factors effective at the moment, including metabolism, conduction from the ground, convection from the air, and radiation from surrounding objects and the sun. Much remains to be done, experimentally, in determining the degree to which such factors as air temperature, ground temperature, solar radiation, humidity, wind velocity, sur-

face color, and similar conditions affect body temperature. An interesting discussion of some of these factors is that of Kelly, Bond, and Heitman (1954, p. 563). However loosely I may employ the word "temperature" in the following discussion, it must be remembered that the snake's own body temperature, as determined by the summation of these exterior conditions, is the really important criterion in controlling and limiting its activity.

If confusion is to be avoided in a consideration of the effect of body temperatures on rattlesnakes, it is essential to distinguish between two viewpoints. The first involves purely physiological considerations: What are the temperatures that a snake can withstand without death or permanent injury; to what temperatures will it voluntarily submit without seeking amelioration; and, finally, what is the temperature zone best suited to its life processes and well-being? The second phase has to do with the habit adjustments of the rattler, whereby it fits the attainment of its necessities of food, reproduction, and protection as best it can into the available temperature conditions. For, in almost none of its habitats are the temperatures at an optimum level continuously. Were the snakes active only when the temperatures were exactly suitable, they would not secure sufficient food, and their season of activity would be too short to complete the reproductive cycle. But by various methods of modifying their activities—both daily and seasonal—so as to profit to the utmost from reasonably favorable temperature levels; through expedients by which they take advantage of differences in microclimate; and finally by continuing to be active at temperature levels that are uncomfortable, and, indeed, by an unexpected fluctuation might even become dangerous, they are successful in maintaining themselves.

In the following discussion I shall first outline the physiological temperature limitations to which the snakes are subject, followed by remarks on how their lives and habits are modified to take advantage of such beneficial temperature conditions as may prevail, whether daily or seasonal.

## PHYSIOLOGICAL TEMPERATURE LIMITATIONS

### MAXIMUM TEMPERATURE LIMITS

Although snakes, as well as other reptiles, are popularly supposed to prefer and seek the hottest weather and exposures, lying out in the sun whenever possible, the fact is that such basking is limited to times of moderate temperatures, for they would be quickly killed by environmental temperatures not particularly uncomfortable to man.

In recent years, a number of experiments have been performed demonstrating the inability of rattlesnakes to withstand direct sunlight on a hot day. My correspondents have supplied the following data on their own experiences:

Having heard about the amount of direct sun heat that a rattler can stand, I was curious to know what this particular subspecies, the Great Basin rattlesnake (*C. v. lutosus*), could take. Accordingly, an adult snake was selected and subjected to the sun rays which the thermometer registered as 91° F.<sup>2</sup> No particular uneasiness was even observed for about 5 minutes; then the reptile became obviously disturbed and restless and tried to crawl away.

<sup>2</sup> Not a valid criterion of the temperature that the snake attained from the ground on which it was placed, to say nothing of the sun's radiation.

However, it was not allowed to do so and its efforts soon became frantic. At the end of 20 minutes it was showing signs of acute distress and at the end of 28 minutes its movements had entirely ceased, except for spasmodic twitchings now and then. *Russell K. Grater, National Park Service, Estes Park, Colo.*



Here at the Canyon I came upon a rattler<sup>a</sup> on the Bright Angel Trail, at Garden Creek, in 1933. Desiring a picture, I hooked him out from the dense growth into the bright sunshine for photographing. It was a very hot July day, about midafternoon; in a very short time he turned belly-up and died before I could pose him and focus the camera. *Louis Schellbach, National Park Service, Grand Canyon, Ariz.*



Having heard that a rattlesnake could not stand the direct rays of the sun for any length of time, I tried out a northern Pacific rattler by tossing it out into a bare sand patch. The day was hot for the elevation (about 3,500 feet). At first, the rattler coiled and was ready to fight, but after about 5 minutes it tried to crawl away and made no further effort to coil when tossed back to the center of the sand patch. It rapidly became weak and at 8 minutes could no longer crawl. During the next 3 minutes it had 3 severe spasms and at the last one it turned over on its back, its mouth flew open very wide, and it made no further movement. This was 11 minutes after I first put it in the sun. *Louis Olive, Alturas, Calif.*



At Poison Meadow, 5,000 feet, Yosemite National Park, on July 8, 1940, on a warm south slope but in the shade, we found a large northern Pacific rattlesnake (*C. v. oreganus*) 44½ inches long. The Yosemite Field School of Natural History questioned the fact that bright direct sunshine would kill a rattlesnake. So we surrounded it and kept it out in the bright sunshine on a barren gravel slope. In 21 minutes of direct exposure to sunshine the snake was dead. Another large rattlesnake that we tested a year previously died in 17 minutes. In another instance where the sunlight was not so intense, the rattlesnake died after 23 minutes of exposure to direct sunlight. *Joseph S. Dixon, U. S. Fish and Wildlife Service, Berkeley, Calif.*

Dr. Seth Benson told me he had tried keeping a sidewinder in the hot desert sun; it died in 11 minutes. He merely removed the bush under which it had been hiding. It became suddenly stiff as if cooked.

Although these experiences involved some differences in the time required to kill a rattlesnake in the hot sun, no doubt correlated with differences in ground and air temperatures, the intensity of the sun's radiation, and the size of the snake (and therefore the rapidity of heat absorption), there is a general agreement that the time of survival under extreme conditions is about 10 to 12 minutes.

Similar experiences have been described in published accounts. Chase (1919, p. 134) found that a sidewinder died in 10 minutes, with an air temperature of 110° F. Benedict (1932, pp. 185, 241) concluded that rattlesnakes could be heated to 37° C. (98½° F.) at low humidity without permanent injury; temperatures beyond this were likely to be lethal, although not always immediately. Swift (1933, p. 150) reported the killing of a northern Pacific rattlesnake in 20 minutes in full sunlight at 5,000 feet altitude in Plumas County, California. Blum and Spealman (1933, p. 150) experimented with infrared and ultraviolet radiation to determine whether any particular wave length of the spectrum was selectively lethal. They concluded that no photochemical reaction was involved but that the fatal result was purely an effect of temperature. They killed a snake in an air bath heated by a hot-water jacket, death occurring in somewhat less than 14

<sup>a</sup> A Grand Canyon rattlesnake (*C. v. abyssus*).

minutes of  $49^{\circ}\text{C}$ . (about  $120\frac{1}{2}^{\circ}\text{F}$ .). The muscles were found to be in rigor. The authors conclude that death is caused by irreversible changes in the tissues produced by excessive temperatures, heat rigor occurring in the muscles of ectotherms at somewhat above  $40^{\circ}\text{C}$ . ( $104^{\circ}\text{F}$ .).

Mosauer and Lazier (1933, p. 149) experimented with three freshly caught rattlesnakes, two sidewinders (*C. cerastes*) and a western diamond (*G. atrox*), all of medium size. The first sidewinder was placed on a level stretch of sandy ground in full sunlight. The surface temperature of the sand was  $55\frac{1}{2}^{\circ}\text{C}$ . ( $132^{\circ}\text{F}$ .), and the air temperature  $35\frac{1}{2}^{\circ}\text{C}$ . ( $96^{\circ}\text{F}$ .). The snake immediately tried to escape toward the shade but was restrained. These attempts ceased at the end of 5 minutes, and after 6 minutes the snake seemed incapable of normal movements, although it was not quite inert. At the end of  $7\frac{1}{2}$  minutes of exposure it seemed quite dead. The body temperature was found to be  $47^{\circ}\text{C}$ . ( $116\frac{1}{2}^{\circ}\text{F}$ .). The second sidewinder was killed in 9 minutes, the body temperature being the same. The western diamond made its final movement after an exposure of  $10\frac{1}{2}$  minutes; the body temperature was  $46\frac{1}{2}^{\circ}\text{C}$ . ( $116^{\circ}\text{F}$ .). The authors report that grave symptoms appear rapidly in the last minutes before death: "During this time the snakes are stretched out fully or almost so, breathing heavily and attempting caterpillar motion. The mouth is opened and closed with a yawning motion, the fangs advanced. Movements in the head region (tongue, fangs) can be observed after the last convulsive wriggling of the body has stopped. The widening of the pupil may be taken as the conclusive sign of death. Rigor mortis sets in almost immediately, is very distinct, and travels from the head tailwards."

Hunt (1934, p. 16) experimented with a northern Pacific rattlesnake in sunlight; it was writhing in 13 minutes and dead in  $17\frac{1}{2}$ . Mosauer (1936a, p. 60) again tested sidewinders, this time with artificial heat in a specially constructed cage, and found that, with air temperatures of  $55^{\circ}\text{C}$ . ( $131^{\circ}\text{F}$ .) and sand temperatures of  $60^{\circ}$  ( $140^{\circ}\text{F}$ .), they died in from  $5\frac{1}{2}$  to  $12\frac{1}{2}$  minutes. The body temperatures at death ranged from  $44.8^{\circ}$  to  $45.7^{\circ}\text{C}$ . ( $113^{\circ}$  to  $114^{\circ}\text{F}$ .) by thermocouple, and measured  $47^{\circ}\text{C}$ . ( $116.5^{\circ}\text{F}$ .) by thermometer. Miller (1937, p. 40) mentions a sidewinder that was killed by heat in  $4\frac{1}{2}$  minutes. Bogert (1939, p. 34) tells of a sidewinder killed in 12 minutes, the ground temperature being  $54^{\circ}\text{C}$ . ( $129^{\circ}\text{F}$ .), and the air temperature about  $38^{\circ}\text{C}$ . ( $100^{\circ}\text{F}$ .). The temperature of the snake was about  $45^{\circ}\text{C}$ . ( $113^{\circ}\text{F}$ .). Lueh (1941, p. 131) thinks that few snakes could survive a body temperature above  $40^{\circ}\text{C}$ . ( $104^{\circ}\text{F}$ .). Cowles and Bogert (1944, p. 286) give the lethal temperature of a sidewinder as  $42.5^{\circ}\text{C}$ . ( $108.5^{\circ}\text{F}$ .) and of a southern Pacific rattlesnake as  $41^{\circ}\text{C}$ . ( $106^{\circ}\text{F}$ .).

Dobie (1949, p. 118) has repeated a highly doubtful story told him of how a coyote kept a sidewinder from retreating to protective shade until it died, whereupon the wise mammal made a meal of it. Roadrunners are sometimes credited with using the same stratagem for the purpose of simultaneously killing and cooking their rattlesnake meals.

Two newspaper accounts mention tests on rattlers that resulted in death in 10 minutes in the sun with an air temperature of  $25.5^{\circ}\text{C}$ . ( $76^{\circ}\text{F}$ .), and another in 10 minutes at  $26.5^{\circ}\text{C}$ . ( $80^{\circ}\text{F}$ .).<sup>4</sup>

<sup>4</sup> Fraser (1936-37, p. 79) performed an interesting series of tests at Deolali, near Bombay, India, to determine the lethal effects of sunlight on snakes. Several—none rattlers, of course—were kept

As we review these tests, we are impressed with the variability of time and temperature required to kill rattlesnakes in the sun. Yet these discrepancies are more presumed than real, for in only a few instances are we given the really critical data, namely, the body temperature reached by the snake at death. For air temperatures are not of great importance when we are dealing with a creature such as a snake, whose body is in intimate contact with the ground. Much more pertinent are the ground temperature, the size of the snake, the colors (reflectivity) of the ground and the snake, together with such conditions as wind velocity, humidity, etc.; for all of these will affect the rapidity of heat absorption by the snake and the body temperature attained, which, after all, is the really decisive factor. Ascertaining the body temperature at the moment of death is a difficult problem, and some of the lethal temperatures that I have quoted are of doubtful accuracy. It is probable that if, in all the tests, the temperature of the snake at death had been ascertained accurately, the variation would not have been great, and the time elapsing before death would depend simply on the rapidity of the heat absorption and the curve of temperature rise to the lethal point.

Attention should be directed to the wide differences between air and ground temperatures as shown by Mosauer's tests. These indicate how relatively unimportant, compared to the ground temperatures, are the air temperatures usually mentioned by observers of field experiments on the killing of rattlers by keeping them in the sun. The snake's body temperature follows the temperature of the ground much more closely than that of the air, as was demonstrated in experiments conducted by R. B. Cowles. He placed sidewinders on substrata at temperatures of 9° to 19° C. (16° to 34° F.) higher than the air temperature. Under these circumstances, the snakes reached temperatures within 1° or 2° C. (1.8° to 3.6° F.) of that of the substratum (8° to 17° C., or 14.5° to 30.5° F., higher than the air temperature) within 5 minutes or so, thus showing the predominant influence of the temperature of the ground, compared with the temperature of the surrounding air. And to indicate how much higher ground temperatures may be than air temperatures, we have the following figures supplied by Court (1949, p. 220) as examples of air-ground differentials in Death Valley and the North American desert areas generally: Air at 5 feet above ground, 125° F. (51.7° C.); at 1 foot above ground, 150° F. (65.6° C.); at 1 inch above ground, 165° F. (73.9° C.); and at ground surface 180° F. (82.2° C.).

It will be noted that several of the experiments previously mentioned were conducted on the sidewinder, the rattlesnake that, judged by the environment in which it lives, might be expected to have a maximum heat tolerance. For the sidewinder inhabits the Mojave and the Colorado or Sonoran deserts, including the floor of Death Valley, where the highest air temperatures ever recorded in

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in the sun under various temperature conditions. They died in from 3 to 85 minutes, all showing the usual symptoms of heat prostration—intertia, head swaying, rolling on the back, distended jaws, labored breathing. The most interesting feature of these tests was that one snake was killed by 85 minutes of exposure on a day when the maximum air temperature in the shade was 76° F., the minimum 36° F., and it was described as being "cold and frosty." Fraser thought the snakes' temperatures were increased by their struggles to reach shade, from which they were restrained. However, it is more probable that the long exposure resulted in a considerable desiccation; but much more important, no doubt, was the temperature reached by the ground surface and the snake itself, both by direct radiation and conduction, of which no record was made.

the Western Hemisphere have been attained. Yet this desert creature seems able to withstand no higher temperatures than other rattlesnakes, and for no longer periods, although its lighter color may reduce the rapidity of heat absorption in sunlight, as compared with some of the darker forms. However, reflectivity is not entirely a matter of visual hue, as I have pointed out elsewhere (Klauber, 1939a, p. 65), for much of the incident radiation is at wave lengths outside of the visual spectrum. Probably the body temperature at which irreversible muscular heat-rigor ensues is virtually the same in all rattlesnakes, at about 45° C. (113° F.), although damage from which the snakes may succumb later may be entailed at lower body temperatures, even down to 43° C. (110° F.), or below, with some variation depending on the duration of the unfavorable temperature. Cowles and Bogert (1944, p. 286) state that the critical maximum body temperature of the sidewinder is 41.6° C. (106.9° F.) and the lethal temperature 42.5° C. (108.5° F.). The corresponding critical maximum temperature for the southern Pacific rattler (*C. v. helleri*) is stated to be 2.8° C. (5.0° F.) lower and the lethal temperature 1.5° C. (2.7° F.) below that of the sidewinder. So far as rattlesnakes are concerned, these tests do not verify Devoe's statement (1951, p. 221) that desert snakes can withstand much higher temperatures than those accustomed to less rigorous conditions.

Certainly the popular idea that a snake relishes high temperatures is anything but true. No doubt the temperature limitations are fixed by the fundamental properties of reptilian muscle and blood, which have not been materially changed through environmental pressure and natural selection to permit a higher tolerance by desert snakes. I have seen no test data proving that any snakes, such as the sidewinding vipers of the Sahara—the horned viper (*Aspis cerastes*) and the sand viper (*A. vipera*)—can withstand higher temperatures than our own sidewinding rattlesnake, which, in turn, succumbs at essentially the same temperature as rattlers inhabiting less torrid areas. Certainly we must question the statement of Stradling (1881, p. 148), who claimed that on the hottest days in the hottest places on earth, he had seen snakes basking in the blazing sun-glare on sand and rocks that would almost blister the hands to touch. Nothing like this has been observed in the American deserts, and there is no reason to believe that Old World snakes have different heat tolerances. I should place the maximum voluntary tolerance of rattlesnakes, according to the terminology of Cowles and Bogert (1944), at about 37° C. (98° F.)—possibly a degree or so higher for desert species and correspondingly lower for those accustomed to more humid conditions.

Statements have appeared from time to time to the effect that some snakes are attracted to campfires, either by the light or heat. For example, Bruce (1790, vol. 5, p. 204; repeated by Martin, 1851, p. 258, and Ruskin, 1875, p. 187) tells us that the horned viper (*Aspis cerastes*) of the Sahara is such a lover of heat that it will approach a campfire at night and burn itself to death in the ashes. Bruce claimed that this was of nightly occurrence, and that there were seldom less than half-a-dozen thus immolated. Dobrizhoffer (1822, p. 298) was another early writer who spoke of snakes—this time in Paraguay—approaching a fire to warm themselves. Payne (1872, p. 223) mentions a copperhead, that, aroused from its winter hibernation, crawled toward a fire for warmth. I was disposed seriously to doubt these stories, but Dr. R. B. Cowles has told me of a sidewinder

that crawled up to a campfire and was only prevented from crawling in by its being repeatedly pushed away from the flames and coals. Whether this is an indication of thermo- or phototropism is not known.

#### MINIMUM TEMPERATURE LIMITS

At the other extreme, the lethal minimum, the transition from at least a permissible temperature to a fatal one is more gradual than at the upper limit; for long before the danger point is reached a zone of lethargy is entered that drives the snake, by instinctive response, to some refuge. This, although it may not improve the temperature experienced, will at least safeguard the animal while helpless and immobile through the stiffening of its muscles. However, it is true that the advent of falling temperatures is likely to be more sudden and unexpected than rising. Rattlers subjected to a falling temperature experience a benumbing lethargy, whereas those in a rising temperature approaching the danger point are active and alert, and should be able to reach a safe refuge. So it is probable that many more rattlers are killed by freezing than by heat, having been rendered incapable of motion when only a few feet or rods from safety. Rattlers enroute to their dens are particularly subject to this danger.

Just what minimum temperatures rattlesnakes can withstand and still survive is not known; probably much depends on the rapidity of freezing and thawing, for it is generally believed that, if the thawing be gradual, they will survive.

Some published statements bearing on this question have been the following: Hoy (1865, p. 432) claimed that, while it is well known that fish will survive freezing, reptiles will not, if they have been completely congealed. Audubon (1827, p. 25) found a rattler stiff as a stone from cold. It was thawed out and survived. A similar observation was made by Tome (1928, p. 115). Goode (1873b, p. 356) reports that Spallanzani kept snakes in a state of torpor in an icehouse for 3½ years, and then restored them to activity. The temperature of the icehouse was not stated. Matteson (1899, p. 671) found a prairie rattlesnake (*C. v. viridis*) stiff from cold and revived it with warm water. He claims that this was repeated daily for 6 weeks, at which time it died, a doubtful story, to say the least. Dorsch (1929, p. 3) quotes a statement of the U. S. Biological Survey to the effect that rattlers will survive freezing if thawed gradually. Bogert (1939, p. 35) reports a Mojave rattler (*C. s. scutulatus*) that survived 10 days in an ice box at 42° F. Davenport (1943, p. 18) says that frozen snakes can sometimes be saved by placing them in cold water and raising the temperature slowly. In January, 1937, the press carried a report of a northern Pacific rattler (*C. v. oreganus*) found frozen stiff near Hollister, California, that was revived by slow thawing. Volsøe (1944, p. 16) expressed the opinion that European vipers might withstand a temperature of a few degrees below freezing. However, he cites a particularly cold winter after which vipers were quite scarce, showing that the mortality had been high.

P. S. Barnhart of La Jolla, California, told me of throwing some frozen young prairie rattlesnakes into a garbage can and later finding that the sun had revived them.

At the San Diego Zoo the following experiment was tried: Two medium-sized Great Basin rattlers (*C. v. lutosus*) were first put in a cold room at 3½° C. (38°

F.). After 6 hours in this room one was transferred to a chill room having a temperature of  $-4\frac{1}{2}^{\circ}\text{C}$ . ( $23\frac{1}{2}^{\circ}\text{F}$ .); the other to a freezer at  $-15^{\circ}\text{C}$ . ( $5^{\circ}\text{F}$ .). After  $15\frac{1}{2}$  hours at these temperatures they were returned to the room at  $3\frac{1}{2}^{\circ}\text{C}$ . ( $38^{\circ}\text{F}$ .), and later to the normal temperature of the reptile house. The first survived; the other died. Another snake of the same subspecies was kept at  $3\frac{1}{2}^{\circ}\text{C}$ . ( $38^{\circ}\text{F}$ .) for nearly 4 days; it was then held at between  $-12^{\circ}$  and  $-11^{\circ}\text{C}$ . ( $10$  and  $12^{\circ}\text{F}$ .) for  $8\frac{1}{2}$  hours, becoming quite stiff. After this it was returned to the  $3\frac{1}{2}^{\circ}\text{C}$ . ( $38^{\circ}\text{F}$ .) room, and then to the reptile house. It showed no signs of life upon thawing and failed to survive the test.

I experimented with 12 prairie rattlesnakes (*C. v. viridis*) from South Dakota that had been captured as they were entering hibernation, and, therefore, were in the best possible condition to withstand cold. They were divided into 4 lots of 3, each lot being placed in a separate aluminum box in a deepfreeze refrigerator, with a compartment temperature of about  $-16^{\circ}\text{C}$ . ( $3^{\circ}\text{F}$ .). At the time they were transferred to the refrigerator the room temperature was  $6\frac{1}{2}^{\circ}\text{C}$ . ( $43.7^{\circ}\text{F}$ .). It was the idea to simulate a cold snap followed by a temperature reversal to ascertain the chance of recovery.

The first snakes were removed at the end of two hours, at which time the temperature in their aluminum box had reached  $-4\frac{1}{2}^{\circ}\text{C}$ . ( $24^{\circ}\text{F}$ .). The snakes were quite soft and seemed inert; however, pinching their tails produced slight body movements. The box was returned to a room at a temperature of  $10^{\circ}\text{C}$ . ( $50^{\circ}\text{F}$ .) and allowed to warm. After 10 minutes, one snake gasped or hissed. After 30 minutes, all could be stimulated into moving slowly; their eyes showed a slight reaction to light. After one hour, one of the snakes everted its tongue upon stimulation, and rattled. The rattle was much slower than usual—it was more like a true rattling sound than the normal hiss produced by the rattle—and was found to vibrate at the rate of 29 cycles per second. At this time one of the snakes was writhing as if in pain, and opened its mouth as if gasping for breath. This snake was still in some distress 2 hours after removal, but one hour later showed no ill effects. Three hours after removal, the room temperature being then  $17^{\circ}\text{C}$ . ( $62\frac{1}{2}^{\circ}\text{F}$ .) and the temperature in the rattlers' box only a little lower, all the snakes were completely alert, and afterwards showed no adverse effects.

The second lot of 3 snakes was removed after 3 hours in the deepfreeze. The temperature in their box was then  $-13^{\circ}\text{C}$ . ( $8\frac{1}{2}^{\circ}\text{F}$ .). All three were frozen stiff in the mid-body section, but were still pliant elsewhere. The box was then allowed to warm slowly and the two larger snakes—one was a sub-adult—were thawed within an hour; none, however, showed signs of life. After another hour, one made slight movements. Three hours after removal, the temperature in their aluminum box being then  $8^{\circ}\text{C}$ . ( $46\frac{1}{2}^{\circ}\text{F}$ .), all three snakes were alive and showed some alertness; they would certainly have been dangerous to handle. Subsequently the two larger snakes made an uneventful recovery, although one was somewhat disco-ordinated in its movements for another hour or so. The smallest snake died. It is possible that in its weakened condition it may have been crushed by the other two, for at one time it seemed to be recovering.

Lot 3 was removed after 4 hours in the deepfreeze compartment. The temperature in the aluminum container was about  $-16^{\circ}\text{C}$ . ( $4^{\circ}\text{F}$ .); yet strangely

enough the two fully adult snakes were quite limp, not partly frozen as was the former lot that had been in the refrigerator a shorter time. The third, which, judged by its size, was about to enter its second winter, was frozen stiff. One hour after removal and transfer to a room at about  $17^{\circ}\text{C}$ . ( $62\frac{1}{2}^{\circ}\text{F}$ .)—although they still remained in their aluminum container, which warmed slowly—no snake showed any signs of life. However, one hour later all made slight body movements upon having their tails pinched. Subsequently the two larger snakes gradually recovered, but the smaller died. Six hours after removal one of the two larger snakes seemed quite normal; but the other, although active and even restive, showed by its wavering head and lack of co-ordination when endeavoring to crawl, that it was still affected, and this condition continued for at least 5 additional hours. Subsequently it recovered completely.

The fourth lot remained 5 hours in the deepfreeze and was removed at a temperature of about  $-14\frac{1}{2}^{\circ}\text{C}$ . ( $6^{\circ}\text{F}$ .). They were frozen solid. Three hours later they still had not thawed; they were completely thawed 5 hours after removal but seemed quite dead. They were then placed in warm water, upon which they squirmed somewhat, but none recovered. Differing from the snakes in the other lots, the smallest snake in this series showed signs of life longer than the others.

I think we may infer from these experiments that prairie rattlesnakes, particularly adults, on the way to their dens, might encounter a sudden drop in temperature that would render them quite helpless and even partly frozen, yet they would still recover if a suitable rise in temperature followed. Whether a rattlesnake, frozen to stiffness throughout, can recover, as has been stated by some published accounts and by several of my correspondents, I do not know. But certainly it has been shown that they can withstand several hours below freezing ( $0^{\circ}\text{C}$ .;  $32^{\circ}\text{F}$ .).

C. M. Bogert has advised me that he maintained specimens of *pricei*, *lepidus*, *horridus*, *molossus*, *atrox*, and *scutulatus* at  $4^{\circ}\text{C}$ . ( $39.2^{\circ}\text{F}$ .) for about 10 days. Those belonging to the first four species lived; the others died. *C. atrox* and *scutulatus* are lowland forms, accustomed to less rigorous winter climates than the others. Additional tests are contemplated; meanwhile it is indicated that there are differences between species in their power to survive protracted cold. Hansen (1954, p. 200) presumed, from the condition and actions of some trapped snakes that were left out in snow overnight, that rattlesnakes—in this case *C. v. lutosus*—are more susceptible to cold than gopher snakes (*Pituophis*), but are less adversely affected than king snakes (*Lampropeltis*) or racers (*Masticophis*).

Bailey (1949, p. 241) found that garter snakes could withstand a minimum temperature of about  $-2^{\circ}\text{C}$ . ( $28.4^{\circ}\text{F}$ .) for from 18 to 28 days.

An important temperature stratum in the life history of the rattlesnake is that which Cowles and Bogert (1944, p. 277) call the critical minimum—the temperature causing a cold narcosis that prevents locomotion, and thus renders the snakes unable to defend themselves against enemies, or to relieve a thermal impasse, if they have not already reached a sanctuary. They found (p. 286) the western diamond (*C. atrox*) capable of stimulated movement at  $14^{\circ}\text{C}$ . ( $57^{\circ}\text{F}$ .), and some natural activity at  $18^{\circ}\text{C}$ . ( $64.5^{\circ}\text{F}$ .). The sidewinder (*C. cerastes*)

showed some natural activity at 16° C. (61° F.), although not normally active until temperatures of 17.5° to 19° C. (63.5° to 67° F.) were reached.

I experimented with several rattlers of various species—a red diamond (*C. r. ruber*), 4 Great Basins (*C. v. lutosus*), 2 southern Pacifics (*C. v. helleri*), and a southwestern speckled rattler (*C. m. pyrrhus*)—and found them capable of activity at temperatures well below those cited by Cowles and Bogert. They were first tested at a constant room temperature of 15° C. (59° F.). Although sluggish and loath to move unless disturbed, they seemed in possession of all their faculties. With a little urging they crawled purposefully; they coiled, rattled, protruded their tongues, and faced me when I moved.

The same snakes were tested after being kept all night at 11° C. (52° F.), the experiment continuing on the following morning in a room at this temperature. They could crawl, a little hesitatingly, but quite efficiently. They could see movements and protruded their tongues in the usual way. All would rattle, although more slowly than customarily; the sound was faint and more of a buzz than a hiss. All snakes would adopt a defensive coil when annoyed, but only the southern Pacific rattlesnakes (*C. v. helleri*) would strike. The strikes were slower and shorter than normal. The forward motion of the head could be seen, as well as the opening of the mouth during the lunge, which is impossible in a normal strike. When turned on their backs, these snakes had no trouble in righting themselves. It was observed that the red diamond (*C. r. ruber*) would only crawl if annoyed; and, if threatened by brushing it with a towel, would hide its head in the center of its coil, instead of adopting a fighting pose. It was noted that, when these snakes elevated their heads for any reason, there was some wavering of the neck.

The same snakes were subsequently placed in the vegetable room at the San Diego Zoo where the temperature was maintained at 5° C. (41° F.). Here they were left for 28 hours, after which their reactions were tested while they were still in the room and therefore subject to no external temperature variation. All snakes, except the *ruber*, would assume a fighting pose if annoyed, and would rattle, but, as before, only the southern Pacific rattlers would strike. The strikes were again short and slow, with the open mouths distinctly seen. One struck only about 8 inches at a person fully 3 feet away, well beyond reach of a rattler of this size even under favorable temperature conditions. That they retained their faculties was shown by their facing any moving object and the frequent protrusion of their tongues; in fact, the Great Basin rattlers elevated and depressed their tongues as rattlers usually do when in their striking coils. The southwestern speckled rattler seemed more affected than the Great Basin or southern Pacific rattlers; it coiled with difficulty, and rattled slowly and weakly, so that almost no sound was audible. It crawled when urged, but the movements were not fully co-ordinated. The snakes could right themselves if turned on their backs. The southern Pacific and Great Basin rattlesnakes seemed to crawl more purposefully than the others; in fact, in another test, a Great Basin rattler kept in a room at 3.5° C. (38° F.) long enough to reach this temperature, crawled around the edge without urging, looking for a place of escape, meanwhile flicking out its tongue.

The fact that these rattlers were quite capable of movement at about 5° C.

(41° F.) is by no means proof that they would escape if caught on their way to the dens at this temperature, for it generally required persistent annoying to stimulate them into movement. It would seem that, although fully capable of motion, they would probably lack the necessary urge or will to reach a refuge more than a few yards away. I should judge that at temperatures of 8° C. (46.5° F.), or below, there would be little voluntary motion even if their safety depended on it, although they would certainly escape if the temperature subsequently should rise again.

The lower limit of temperatures permitting muscular motion upon stimulation is not known; it probably lies between 1.5 and 4.5° C. (35 to 40° F.). We may seriously doubt the figure of 22° F. given by Coahoma (1902, p. 64) as representing the body temperature of a snake in which he detected movements.

Swanson (1952b, p. 168) noted that captive timber rattlers were moderately alert when the air temperature was 57° F. (13.9° C.) and the floor of the cage was 60° F. (15.6° C.). Fitch and Glading observed juvenile northern Pacifics active and alert when the air temperatures were 64° and 66° F. (17.8° and 18.9° C.).

From all of these data, I should conclude that adult rattlesnakes, if thawed slowly, may recover from a few hours of subjection to a temperature of -16° C. (4° F.), and can endure 3° C. (37.4° F.) for some time, measured in days or more. They can crawl and show some degree of co-ordination at body temperatures of 5° C. (41° F.), but prodding is required to make them move.

Cowles and Bogert (1944, p. 287) found the minimum voluntary tolerance—resulting in retreat underground—of the western diamond rattlesnake (*C. atrox*) to be 18° C. (64.5° F.) and of the sidewinder (*C. cerastes*) 17.5° C. (63.5° F.). Judging from field experiences, I should place this temperature zone somewhat lower, say at least 16° C. (61° F.) for these desert species, and but slightly higher for other forms found elsewhere in the United States. After all, the word "voluntary" depends on circumstances and the snake's necessities. I should judge that a rattler that had not yet obtained food following emergence in the spring would be voluntarily active at a lower temperature than under other circumstances.

#### OPTIMUM TEMPERATURE RANGE

Finally we come to what Cowles and Bogert call the normal activity range—the range of greatest comfort and bodily well-being. I should place this—at least for our Nearctic rattlesnakes—at between 26½° C. and 32° C. (about 80° and 90° F.), centering probably at about 29¼° C. (85° F.). At this temperature the snakes are alert, their muscular activity well toned, and bodily processes—digestion and gestation—at an optimum. Again, these temperature levels refer to the internal temperatures of the snakes—not to some single exterior criterion, such as the air temperature in the shade.

The following are some of the opinions expressed by my correspondents on this point:

In the Lower Sonoran Zone of Arizona general observations would lead to the broad statement that rattlesnake activity is governed by ground and air temperature and relative humidity, rather than time of day or night. About 80° F. seems to be an optimum ground and air temperature. During cloudy days when this condition exists, they are

active. During the evenings when the ground and air are cooling slowly, the snakes have the longest continuous period of these conditions, coupled with the most active period of the rodents upon which they prey. *Lee W. Arnold, U. S. Fish and Wildlife Service, Denver, Colo.*



Rattlesnakes prefer temperatures of about 90° F., and are most active at this temperature. *Phil Kennedy, U. S. Forest Service, Douglas, Ariz.*



Rattlesnake activities seem to be governed to quite an extent by the weather and temperature, either day or night. That is, at a temperature between 80° and 90° F. they are most active. Weather either hotter or colder than that mentioned seems to be unfavorable for them. *Glenn Flathers, U. S. Forest Service, Camp Crook, S. Dak.*

Among the published accounts setting forth the preferred<sup>5</sup> temperature ranges are those of Fitch and Glading (1947, p. 107), who specify 80° to 90° F. for northern Pacific rattlers at the San Joaquin Experimental Range. Cowles and Bogert (1944, p. 286) found the sidewinder to prefer temperatures of 31° to 32° C. (88° to 89.5° F.), when given a free choice of a graded series of temperature zones. As would be expected of this desert reptile, this is toward the upper limit of the preferred temperature zone that I have given for rattlesnakes as a group.

It is probable that, for vivariums, slightly lower temperatures are desirable than seem to be preferred by snakes in the wild, especially since they need hunt for neither food nor mates. Lederer (1936, p. 135) kept rattlesnakes at from 25° to 32° C. (77° to 89.6° F.). He considered a daily change of temperature desirable and allowed it to fall to 18° C. (64.4° F.) nightly. Lueth (1941, p. 130) recommends about 25° C. (77° F.) for snakes. Allen and Neill (1950d, p. 7) suggest about 24° to 26° C. (75° to 80° F.). C. B. Perkins, at the San Diego Zoo, prefers a slightly higher average figure—an air temperature of about 27° C. (80° F.) in the cages. The temperature should be adequate to promote digestion and to afford adequate bodily well-being to repel parasites and disease. But an excess temperature speeds up the body processes and probably shortens life. As Rodbard (1948, p. 414; 1953, p. 138) has pointed out, an increase in body temperature increases metabolic activity, as indicated by oxygen consumption, general activity, respiratory and heart rates, blood pressure, and circulatory rates. All of these are essential to a rattlesnake in the wild searching for food and mates, and ever on the alert against possible attack by enemies. But in captivity a slower and more placid existence is to be desired, and probably leads to a longer life.

### TEMPORAL VARIATIONS IN HABITS

Having discussed the physiological temperature limitations of rattlesnakes and their temperature preferences, I shall proceed with the second phase of the discussion, namely, the effect of temperature on their habits; how their seasonal and diurnal activities are influenced by temperature; their various methods of taking advantage of differences in microclimate; and the extent to which they endure

<sup>5</sup> There is a general objection to the use of the term "prefer" as having an anthropomorphic implication. Yet, as Cowles and Bogert have shown, where several temperature zones are available, rattlers do show a preference, that is, they exercise a choice, and it is difficult to describe their responses to temperatures and temperature changes without inferring preference or selection.

uncomfortable and even dangerous temperatures to attain their life necessities of food, mates, and security from enemies.

To this end, they have evolved a variety of expedient instincts and may react in various ways to take advantage of favorable weather and to protect themselves against its deficiencies. This requires both seasonal and daily adaptations or adjustments to thermal conditions; it involves going underground when it is too hot or too cold\* on the surface; and involves taking advantage of whatever time of day or night produces the most favorable temperatures for surface activities, always provided, however, that the main objectives are not thereby neglected. Where food or mating urges require activity under unsatisfactory temperature conditions, a compromise is made and the snake endures discomfort and even, to some extent, danger, to secure the primary objective.

It should be pointed out that, regardless of any willingness to pursue its activities under unfavorable temperature conditions, a minimum duration of adequate temperatures must be available if the species is to survive; for such temperatures—and they must emanate from external conditions—are necessary for the life processes of digestion and gestation. To secure these periods of adequate temperatures the snake indulges in basking, although with some sacrifice of safety from enemies.

#### SEASONAL VARIATIONS IN ACTIVITY

Although rattlesnake activities are strongly affected by temperatures—using the term in the broad sense of the thermal impact or flux from the surroundings that produces a specific body temperature—this does not mean that rattlers are most active when the weather is most propitious. On the contrary, spring is the time of greatest activity, for they are hungry then after their long winter fast, and, in most areas, this is the mating season as well. So, although spring is a period of below-optimum temperatures in many areas, the rattlers' activities are then at a maximum, and in some areas they not infrequently imperil their own safety by becoming active too early.

Beginning in 1923 I compiled data on the incidence of snakes in San Diego County, California, tabulating their occurrence by months and life zones (Klauber, 1923, table 1; 1931, table 1; 1939, table 16). This survey comprised some 17,000 snakes, of which 3,637 were rattlers. The rattlesnake statistics are set forth in table 7:1. I have omitted from this table 2 specimens of *C. atrox* included in former tables, but now believed to have been incorrectly incorporated in the San Diego County census.

These compilations are premised on records of snakes presented to the Zoölogical Society of San Diego and the San Diego Society of Natural History, and on specimens collected or observed in the field by the writer or his associates in these institutions. Since the rattlesnakes of San Diego County do not congregate for denning, the statistics have not been distorted by large catches at dens. There is undoubtedly some distortion owing to the increased human activities in spring and summer, for, after all, snakes are collected when people are roaming about over the hills; however, this distorting factor is not believed to be a serious one, since, in this area, people are outdoors much of the year.

The concentration of rattlesnakes in the spring months, centering in May, is

\*It may also be too cold for activity below ground, but at least the snake is protected from enemies while comatose from cold, and, if it goes deep enough, from death by freezing.

TABLE 7:1  
MONTHLY DISTRIBUTION OF RATTLESNAKES COLLECTED OR OBSERVED IN SAN DIEGO COUNTY, CALIFORNIA, 1923 TO 1947, INCLUSIVE

Month	Number of snakes					Distribution in per cent				
	Southern Pacific	Red diamond	Southwestern speckled	Sidewinder	Total	Southern Pacific	Red diamond	Southwestern speckled	Sidewinder	Total
January.....	22	12	..	..	34	1.3	0.9	...	...	0.9
February.....	30	35	1	2	68	1.7	2.7	0.3	0.8	1.9
March.....	170	150	12	2	334	9.9	11.5	3.3	0.8	9.2
April.....	309	352	46	59	766	18.0	26.9	12.6	23.8	21.0
May.....	353	249	89	102	793	20.6	19.1	24.3	41.1	21.8
June.....	242	159	90	39	530	14.1	12.2	24.6	15.7	14.6
July.....	158	100	42	19	319	9.2	7.7	11.5	7.7	8.8
August.....	142	90	41	2	275	8.3	6.9	11.2	0.8	7.6
September.....	105	71	26	15	217	6.1	5.4	7.1	6.1	6.0
October.....	118	58	6	5	187	6.9	4.4	1.6	2.0	5.1
November.....	37	20	2	3	62	2.2	1.5	0.5	1.2	1.7
December.....	30	11	11	...	52	1.7	0.8	3.0	...	1.4
Total.....	1,716	1,307	366	248	3,637	100.0	100.0	100.0	100.0	100.0

clearly evident, although one of the four subspecies found in the area, the red diamond (*C. r. ruber*), has a slightly earlier peak in April. Altogether, more than half the annual catch is made in the three months of April, May, and June; and this same proportionate distribution is noted year after year, with a slight delay, of two weeks or so, evident in years of unusually heavy spring rains.

It is important to observe that this spring peak of activity seems to be produced in spite of, rather than because of, favorable thermal conditions, at least in some of our southwestern areas. True, the temperatures are nearer the optimum than in the winter, but, by and large, they are not so propitious as in the summer. For, in the coastal belt, even the diurnal temperature rarely reaches the preferred zone of 80° to 90° F. in the summer; and although, in the inland valley and foothill zones, the diurnal range is usually within this temperature zone in summer, it is generally below in the spring. It is only in the desert area that the spring can be considered the most favorable season from the thermal standpoint, and even here the nocturnality of the snakes causes them to be most active at temperatures below the optimum. A further proof that the season rather than the temperature is controlling, is evident in the lack of a corresponding peak in the autumn when the thermal conditions are again equivalent to those of spring.

Although there are available no statistics of any other area covering so long a period as these from San Diego County, there is ample proof that spring is the season of maximum activity of other species and in other areas. At one time the San Diego Zoo received large numbers of rattlesnakes collected by section crews working along the Santa Fe Railroad in central Arizona. The rattlers were caught in greatest numbers in the spring—earlier at the lower elevations, later at the higher. The forms most plentifully represented were the western diamond (*C. atrox*), the Mojave (*C. s. scutulatus*), the Arizona black (*C. v. cerberus*), the Arizona prairie (*C. v. nuntius*), the northern blacktail (*C. m. molossus*), and the southwestern speckled rattler (*C. m. pyrrhus*).

Hunting in areas other than southern California, my associates and I have found the collecting uniformly best in the spring; this refers to such species as the western diamond (*C. atrox*) and the Colorado Desert sidewinder (*C. c. laterorepens*) in the Colorado Desert, and the Panamint rattler (*C. m. stephensi*), the Mojave rattler (*C. s. scutulatus*), and the Mojave Desert sidewinder (*C. c. cerastes*) in the Mojave Desert.

Fred Lewis, in the Cape Region of Baja California, employed Mexican collectors with great success, in the month of April, to round up large numbers of the San Lucan diamond (*C. r. lucasensis*), with lesser numbers of the other two rattlers occurring in that district—the San Lucan speckled rattler (*C. m. mitchelli*) and the Lower California rattlesnake (*C. e. enyo*). The snakes of that area do not gather in dens, so this was not a hibernating aggregation.

Professional collectors at Indian Wells, California, and Mohawk and Oracle Junction, Arizona, informed me that they found rattlers most plentiful in the spring, even as early as March in some places.

Fitch and Glading (1947, p. 106) and Fitch (1949a, p. 521) found that the northern Pacific rattlesnakes (*C. v. oreganus*) on the San Joaquin Experimental Range were most plentiful in April, May, and June. Females and young reached their peaks of activity slightly later than adult males.

Fautin (1946, p. 294) found that the activity of the Great Basin rattlesnake (*C. v. lutosus*) in western Utah did not reach so sharp a peak as has been indicated for other forms in other areas.

The spring peak of activity is not restricted to the rattlesnakes of the Southwest, or, indeed, to rattlesnakes. On the contrary, it is apparently universal. Our San Diego County studies (1939, table 16) have shown it to be equally characteristic of the many other species of snakes found in this area; and our collecting experiences have shown the same conditions to exist in other areas throughout the Southwest. Atkinson and Netting (1927, p. 42) reported that 75 per cent of the massasaugas collected in Pennsylvania were taken in April and May.

Rattlesnake activity is not to be judged entirely by the frequency with which snakes are caught, for they are most evident when basking, but this is not always to be taken as a criterion of activity, which might more properly be considered to be cruising about in search of food, mates, or hiding places. This is particularly true at the time of entering and leaving hibernation, in those places where the rattlers congregate in dens. Here the snakes lie about in the sun for a few days before going permanently below ground in the fall, and similarly they take advantage of the first warm hours in the spring. Anyone coming upon such aggregations might judge this a time of peak rattlesnake activity; and, quantitatively, any tabulation of collections by months would show sharp peaks at such times. For example, C. B. Perkins, collecting at three prairie-dog towns near Platteville, Colorado, took 408 prairie rattlers (*C. v. viridis*) within a period of 22 days in the autumn of 1931. He actually collected only on 10 days, for the dens were unvisited on 12. But during the previous summer he had visited the towns almost weekly (about 14 trips) and secured only 2 rattlers. This remarkable discrepancy was the result of three causes: (1) the rattlers had spread to their summer ranges and were therefore dispersed rather than concentrated; (2) there was a summer slump in activity; and (3) to whatever extent there was activity in the summer, it was largely nocturnal and therefore the snakes were not in evidence. Wilfred T. Neill advised me that the capture of eastern diamondbacks (*C. adamanteus*) in northern Florida reaches a peak in February, not because the snakes are most active at that time, but because they spend a considerable time at that season basking at the mouths of the gopher-tortoise holes in which they seek their winter seclusion.

Oliver (1947, p. 8) has reviewed the data published on the seasonal variation in snake activity, with a contribution of his own on the incidence of the tree snake *Thalerophis richardi nigromarginatus* in the vicinity of Iquitos, Peru. This snake shows a conspicuous March peak notwithstanding the very slight variation in the monthly mean temperature at this locality. While the rainfall reaches a maximum in March, there is no really dry season, some rain falling in every month.

The major difference between our San Diego results, and those of other areas from which tabulations are available, is that the latter all showed minor fall peaks of activity, a condition observed in only a few San Diego County subspecies, and one not evident among the rattlers, with the possible exception of the sidewinder (*C. c. laterorepens*). Fall peaks may be caused by searches for food when the snakes are accumulating their winter fat reserves, or by the prevalence of numbers of young immediately after hatching or birth in the early autumn.

Oliver (1947, p. 13) has given the following comprehensive summary of the reasons for the seasonal fluctuations in the number of snakes observed: (1) aggregation in the vicinity of dens; (2) mating activity; (3) increased food requirements following hibernation, decreasing later; (4) basking; (5) variations in protective cover provided by deciduous vegetation; (6) change from diurnal to crepuscular or nocturnal habits; (7) rainfall; (8) seasonal variations in human activity; (9) oviposition; and (10) appearance of young-of-the-year.

The popular supposition that rattlesnakes are lovers of hot weather, whereas spring is really their season of maximum activity, leads to reports, almost annually in the press, that "rattlesnakes are out unusually early this year." This is particularly true in southern California, where the rattlers do not congregate in dens, but are first seen singly, or in pairs or trios, lying about the cactus patches and granite outcrops, sunning themselves quite carelessly and conspicuously. As this is coincidentally the wild-flower season, it is natural that they should be noticed by motorists and hikers. The following is a typical newspaper report. It is from the *San Diego Union* of March 28, 1926: "Snakes are out early this year and apparently there is a goodly crop. At least reports received from various motorists and campers would indicate that there are many snakes out this season. . . . Many old-timers of this section say that an early appearance of snakes is an indication of the end of the winter and the finish of the rainy season."

#### EFFECTS OF REPRODUCTIVE CYCLE ON SEASONAL ACTIVITY

The reproductive cycles of rattlesnakes affect their seasonal activities in three principal ways: The increased activity of the mating season; the decreased roaming of the females when heavy with young but under the necessity of maintaining a temperature adequate to gestation; and the roving of the young themselves after their appearance.

Along the southern border of the United States, and in northern Mexico, rattlesnakes normally mate in the spring, soon after emerging from hibernation. In some instances they have been observed mating at the dens; but it is probable that mating more often occurs after they reach their summer ranges. At any rate, mating coincides with their heaviest feeding period, so that these two conditions combine to produce the annual season of maximum rattlesnake activity.

In the northern latitudes where biennial broods are the rule (see p. 686), the mating season may be largely confined to autumn, and seasonal activities are correspondingly affected.

When the females are heavy with young in the summer, they become increasingly secretive so that many more males are encountered than females. At such times about twice as many males as females are seen abroad, whereas at the dens the males outnumber the females by only about 10 per cent (Klauber, 1936b, p. 11). Fitch and Glading (1947, p. 107; Fitch, 1949a, p. 522) noted that the activities of large female northern Pacific rattlesnakes were much reduced from July to October. In one year, out of 21 females of this size, 18 were taken before July 1.

The young rattlesnakes in most areas are born between August 1 and October 15, centering in mid-September. The young are quite active immediately following their appearance, for the securing of food is almost essential to their surviving

the following winter. They are both hungry and inexperienced, and consequently careless of concealment, so that they frequently are found roaming in the daytime. R. B. Cowles calls attention to the fact that there is a widespread phenomenon of dispersal of the young of land vertebrates in the search for shelter and dens of their own, and this may also be effective in making them careless. Fitch (1949a, p. 522) noted that young northern Pacific rattlers emerged earlier in the evening than adults. He also reported that the young rattlers reached a spring peak of activity somewhat later than the adults. The adults were often discovered in April, as they were then mating, whereas the young were caught in greatest numbers in May.

Jackley, Perkins, and others who have studied prairie rattlesnakes (*C. v. viridis*) at their dens report the large males as the first snakes to emerge. The same early activity of the males was noted by Fitch (1949a, p. 521) at the San Joaquin Experimental Range, although there the snakes do not aggregate in denning, but seek seclusion singly or in small groups.

#### DENNING DATES AND THE RISK OF IMMOBILITY

It hardly needs to be stated that, with the close dependence of rattlesnakes on exterior temperatures, the dates on which they enter and leave hibernation—the length of their active season—depend on latitude and altitude and other features that affect local climatic conditions. Volsøe (1944, p. 11) has shown that the European viper is active during seasons that vary from as long as 270 days per annum in southern Europe, to only 90 days in the north.

Under the mild conditions that exist in coastal southern California, rattlers are out of sight most of the time from December 1 to March 1; but whenever there is a warm spell, raising the temperatures into the 80's for several days, the snakes may be found sunning themselves on the rocks. Similar conditions occur elsewhere along the southern border of the United States:

We saw rattlesnakes in the Rio Grande Canyon, above the junction with Cochiti Creek, up on the hillsides sunning themselves in the middle of winter. The hillsides are very dry and littered with lava formations and brush. J. A. Rodriguez, U. S. Forest Service, Pecos, N. Mex.

At Somerest, Texas, A. J. Kirn kept a record for nine years of the date when the first western diamond rattler was encountered, with the following results:

1924, April 24	1930, April 30	1939, April 15
1926, April 21	1935, April 13	1945, March 4
1927, April 27	1937, March 10	1947, February 12

Occasionally rattlers are found active in the winter in areas of a more rigorous climate, as for example, in New Jersey (Conniff, 1948, p. 49) and Pennsylvania (*Pennsylvania Game News*, vol. 22, no. 11, p. 30; and vol. 23, no. 1, p. 52, 1952).

Fitch and Glading (1947, p. 107; Fitch, 1949a, p. 517) reported a general emergence from hibernation of the northern Pacific rattlers (*C. v. oreganus*) on the San Joaquin Experimental Range, Madera County, California, on the following dates: 1938, April 11; 1939, March 16; 1940, March 19. The effect of the severe 1938 winter is indicated. A rise in temperature above 70° F. was usually a signal for a general emergence.

Vetas (1951, p. 16), in a study of the activities of Great Basin rattlesnakes (*C. v. lutosus*) at a den near Salt Lake City, observed in 1949 that the first rattler appeared on April 12; only five came out before April 21. Peaks of emergence were observed on May 3, 10, and 23. The last rattlers left the den on May 28. These dates were somewhat, but not solely, related to warm spells. An air temperature of 65° F. (18.3° C.), as a daily maximum, seemed to be a signal for the exodus to begin; at this time the body temperatures of the emerging snakes were about 48° to 50° F. (8.9° to 10.0° C.). Although rattlers began to come out in numbers when the maximum daily temperature reached 65° F. (18.3° C.), the peak of emergence occurred at 74° F. (23.3° C.), and practically all had left when the maximum diurnal air temperature reached 83° F. (28.3° C.). The emergence in the spring was found to be more closely regulated by warm daytime temperatures than was the ingress in the fall, which was spread over a wider range of daily temperatures.

A. C. Mackie has this to say about the seasonal activities of the northern Pacific rattlesnakes near Vernon, British Columbia:

The date of their emergence from the dens naturally varies with the season. In 1931, 1932, 1933, 1934, and 1936, the date varied from April 21 to 26, though it is probable that earlier dates would have been recorded had I visited the dens sooner. In 1935, 1937, 1938, and 1939, it varied from April 10 to 14. Spring came earlier the next 3 years, and I killed my first snake on March 24, 1940; March 12, 1941; and March 30, 1942. In 1943 they first emerged on April 10, in spite of their unusually early hibernation and the severe cold of the winter. The date for their final appearance is less definitely known, as I seldom hunt them in the fall. In 1931, 1932, and 1934, the last were seen between October 1 and 11. In 1937 one was killed on October 24, an unusually late date. Mid-October roughly marks the close of the season. Normally they are abroad for just about 6 months.

Subsequently, Mr. Mackie sent me each year a record of the date when the first and last rattlers were seen, as follows:

Year	Earliest date	Latest date
1945 . . . . .	April 1	October 6
1946 . . . . .	" 15	September 10
1947 . . . . .	" 5	" 26
1948 . . . . .	" 8	" 12
1949 . . . . .	" 10	" 11
1950 . . . . .	March 30	" 28
1951 . . . . .	April 7	" 19
1952 . . . . .	" 13	" 24
1953 . . . . .	" 6	October 11
1954 . . . . .	" 17	" 16

I have detailed elsewhere (p. 560) the results of C. B. Perkins' experiences with the prairie rattlesnake (*C. v. viridis*) in the vicinity of Platteville, Colorado. In two successive years he found the peak ingoing concentrations on October 13 and 14; and the outgoing about April 17 to 19.

A. M. Jackley advised me that the period of emergence of this subspecies in South Dakota extends from April 25 to May 15. There is more variation in the fall because of variable weather conditions, the dates of aggregation ranging from September 20 until almost the end of October.

Sweet (1954, p. 55) says that in Montana the prairie rattlesnakes come out to lie around the den entrances about May 1, but it must be sunny and not too

windy or they fail to appear. They arrive back at the dens as early as mid-September, but, again depending on the weather, they may not disappear for good until mid-November.

The following are a few miscellaneous observations on early and late records:

Rattlers appear in the spring beginning the latter part of April, and have been seen as late as December 2. This last date was on the Madison River in 1939. *Merlin R. Stock, U. S. Forest Service, Twin Falls, Idaho.*



The earliest I have seen a Pacific rattler in northern California was on the 24th of April on the Klamath River near Hornbrook, and the latest was in October shortly before the close of deer season (October 15), at the south end of Tule Lake. However, I once killed a Great Basin rattlesnake on the 24th of October about 60 miles north of Ely, Nevada, when the temperatures were going down to around 10° or 12° F. above zero at night. *Louis Olive, Alturas, Calif.*



One rattlesnake was observed and killed as late as October 27, 1937, a cold, damp day. It was crawling around very sluggishly near the east fork of Squaw Creek. Usually they are not seen so late in the season, unless it is hot, dry weather. Another was heard on October 24th, but escaped in the rocks. *A. L. Parker, U. S. Forest Service, Ydalpom, Calif.*

Conniff (1948, p. 49) places the dates of entrance of the timber rattler (*C. h. horridus*) in New Jersey at mid-September, and their emergence at mid-April. Minton (1950, p. 322), writing of the eastern massasauga in Indiana, says they emerge from hibernation late in April, but stay at the dens for a month before dispersing. They are back at the dens late in August but do not go underground finally until mid-October. This is a longer stay at the dens than is believed customary with other species.

Cowles (1941, p. 135) reports that, in the vicinity of Indio, California, the sidewinder (*C. c. laterorepens*) usually comes out during the first week in April. A western diamond (*C. atrox*) was found active as late as December 18.

The risk of a sudden cold spell is more serious in the fall than in the spring, for in the former case the rattlers may be chilled and immobilized at a distance from the dens and the succeeding temperatures will tend to be lower, while in spring they are more likely to be caught at the dens where they need only go back underground for safety, and the trend is toward rising temperatures. It is obvious that the shorter the active season the more chances rattlers must take with adverse weather, in order to fulfill their food and mating requirements in the limited time available.

That this matter of enforced immobility is often of vital importance to snakes beset with a sudden cold snap, while on their way to the dens for hibernation below the frost line, is evident from the following:

Early one October about three inches of snow had fallen and comparatively few rattlers had reached the dens. Immediately following this storm, the weather became delightfully warm during the day and the snow quickly melted. The second day, after practically all of the snow was gone, a party of several men visited a den in Stanley County about noon. This den was situated on the west bank of a deep gulch and the snakes coming from the east had to cross it. It so happened that a strip of snow about a yard wide and extending along the bottom of this ditch had not melted. Singular as it may seem, eleven rattlers, mostly of large size, attempted to cross the snow but couldn't make it. One was stretched out across the snow, too stiff to coil, and the others lying close by could scarcely move. So

these snakes were unable to reach the den which was no more than 300 feet away. At the den there was a large number that had not encountered this obstacle. *A. M. Jackley, Pierre, S. Dak.*

It is to be presumed that these snakes would have revived with the warmer day and reached the den; but there must be many cases, and Mr. Jackley has reported some, in which the weather change was too protracted and the temperature reached too low to permit recovery.<sup>7</sup> The following is an illustration:

Last winter, Joseph Toulouse and I were on a routine inspection at Chaco Canyon National Monument. While climbing one of the low hills, we were startled by the sight of a rattler stretched up the hill. We saw at once that there was no need to be alarmed because the snake's head was in a patch of snow. It had apparently been trying to reach a small ledge and had succumbed to the cold. A snowstorm had frozen its carcass and it had gradually dried out but still looked very lifelike. *Louis R. Caywood, National Park Service, Santa Fe, N. Mex.*

Short temperature drops resulting in immobility are of little importance to a snake unless dangerously low levels are reached or the snake is attacked by some enemy while helpless. It is by no means unusual to find snakes chilled into complete lethargy in the early morning during their active seasons. This is even the case in mountain areas in the tropics (Pitman, 1938, p. 9) and is of frequent occurrence in desert mountains (Merriam in Stejneger, 1893, p. 217).

Rattlers are occasionally seen on, or close to, snow banks. Kauffeld (1934a, p. 350) mentions a blacktail (*C. m. molossus*) found in the Huachuca Mountains late in November with a thin covering of snow on the ground. I have one report of a northern Pacific rattler (*C. v. oreganus*) on the edge of a patch of snow in Placer County, California, in June; and a Great Basin (*C. v. lutosus*) on four inches of snow in Idaho at an elevation of 7,000 feet. Nelson S. Stone, of Camptonville, California, writes me that he has seen rattlers, upon emerging from their den following two days of exceptionally warm weather in early April, actually crawl over snow drifts.

Babcock (1925, p. 9; Teale, 1951, p. 70) tells of a snake catch reported in Massachusetts in 1844. A snake hunter built a fire before a den, lured the snakes out, and then flung them in the snow, which chilled them so that none escaped. But it may be questioned whether any snakes would emerge from a den because of the heat of a fire.

Enforced immobility through chilling in a refrigerator is sometimes used in handling snakes, as, for example, when a minor operation is required, or to quiet a rattler for photographing.

It should be noted that infringing on or extending the voluntary minimum, under spring conditions on the desert, is fraught with less danger than encroaching on the voluntary maximum, and the need of violating either minimum or maximum occurs at seasons of greater activity with respect to the former than the latter. For spring in particular is the season of greatest rattlesnake activity, because of the demands of hunger after hibernation, and of mating; and autumn is also a time of feeding in preparation for winter. Summer, on the contrary, is a

<sup>7</sup> Pausanias, the Greek traveler, writing in the second century A.D., made the same observation on the snakes of Arcadia, for he noted that "the snakes die that are cut off by the snow from their holes" (Jones translation, 1918-35, vol. 3, p. 425).

season of relative inactivity, so that the rattlers are not under pressure to trespass on the diurnal dangers of excessive heat. Thus I think it likely that most rattlesnake species find it expedient to endure temperatures colder than the optimum more often than warmer. One seldom finds a rattlesnake under conditions that seem notably hot, whereas it is not unusual to find them out when the temperatures are surprisingly low. For example, on April 15 at 10:20 P.M., at Garnet in Riverside County, California, I found a Colorado Desert sidewinder (*C. c. laterorepens*) out on the road with the temperature 59° F. (15° C.). There was a strong, cold wind sweeping the ground, and I have little doubt that the snake's body was at about the same temperature. Although it moved sluggishly, it was in no difficulty.

In summary, it appears that the active season of rattlesnakes in the United States varies from 5 months, in the north and at higher elevations, to 9 or 10 months, or even longer, along the southern border. Where the seasons are less severe, the time limits of activity are less sharply drawn. There is a sharp peak of activity of rattlesnakes in the spring; this peak is not the result of favorable temperatures, and, in fact, in many areas, occurs despite unfavorable temperatures, but it is the time of mating and of the heaviest food requirements.

#### RATTLESNAKES AS WEATHER INDICATORS

Though rarely, rattlesnakes have been considered weather indicators—reptilian ground hogs of a sort. T. C. Elliott (1910, p. 385) quotes the journal of Peter Skene, written November 18, 1828, on the upper reaches of the Humboldt River: "At this season last year we were surrounded by snow and ice. Weather is mild as September and the rattlesnakes have not yet gone. This gives us hope the winter will be mild."

Some of my correspondents have suggested that rattlers were seen bound for their dens at early dates when particularly cold winters were experienced, even before the effects of the coming severe season were evident.

Whether rattlesnakes are weather prophets I cannot say, but in 1942 they arrived in the neighborhood of their dens toward the end of August, that is, nearly a month before their normal time; and the ensuing winter was unusually long and severe. It may have been merely a coincidence. *A. C. Mackie, Vernon, B. C.*

Although their dates of entering and leaving hibernation are undoubtedly affected by seasonal variations, there is no real evidence that rattlers can anticipate adverse conditions in the manner so often attributed to animals. In fact, the frequency with which they are caught and immobilized on the way to their dens by a sudden cold snap should be convincing evidence that they lack this reputed power.

#### SUMMER MIGRATIONS AND ESTIVATION

Migrations of rattlesnakes toward their dens in the fall and away from them in the spring have been discussed elsewhere (pp. 587 and 603). It is probable that they must sometimes travel as much as 2 miles or more to reach their dens, but ordinarily the distance is probably less than a mile. Since suitable rocky outcrops are usually on hillsides, the spring migration is likely to be downhill to the valleys below.

Several of my correspondents suggest that there may also be summer migrations, for example, downhill for water in dry seasons, or to mountain tops for coolness. Presumably these migrations, if at all regular and affecting any considerable proportion of the rattlesnake population, must depend on local topographic and seasonal conditions.

During the later summer, and early fall, many rattlers move from the high elevations, and from the ridge tops, down along streams and into the cooler, shady coves. *John H. Stanley, U. S. Forest Service, Andrews, N. C.*



Weather conditions during the summer season have a considerable effect upon the range of rattlesnakes. The past season having been quite wet and cold, naturally the snakes were held to a lower level than would have been the case during a drouth or dry period, when they are found at higher elevations. *F. L. Archer, Lander, Wyo.*



Along in the early summer rattlers come out of the mountains down into the lower country and valleys, where the ground is wetter and cooler, and here they stay until it starts to get cold in the fall of the year. They then go back into the hills to their dens. *Ollie Cox, U. S. Fish and Wildlife Service, Eureka, Nev.*



After rattlers come out of their dens, in the spring, they migrate to higher country where it is cooler and also there is more moisture. *W. D. Royster, U. S. Forest Service, Paulina, Oreg.*



One June we were disturbed by rattlesnakes crawling into our camp between three and four in the afternoon. This camp was located in the Sierras about 20 miles above the Calaveras grove of Big Trees. The forest ranger called it a "rattlesnake summer." As you know, we experience such cycles of abundance. It is when one of these cycles occurs that the snakes move down from the hills onto the valley floor. I have always felt this to be caused by a shortage of food in their natural feeding range, a result of overpopulation. *Esther L. Guthrie, Sacramento, Calif.*

That rattlesnakes estivate—using the term to indicate a complete suspension of activity—is to be doubted, although a reduction of activity during the summer is quite normal and has been noted by many observers. Hibernation is forced, in most areas of the United States, by exterior conditions that would be fatal at any time of the day or night. Such a condition rarely exists in summer for more than a few days; for while the diurnal temperatures, for long periods, reach levels beyond the ability of any snake to withstand, there is nightly a sufficient fall of temperature, both of ground and air, so that snakes can and do emerge from their subterranean refuges if their bodily necessities require. They are not prevented from doing so owing to any lack of adaptation for nocturnal forays, for they are, in fact, well equipped for night activity, and adopt such a regime in any season when daytime temperatures are less favorable than night. Another reason for the long periods of subterranean seclusion is the increased humidity down holes, which reduces moisture loss.

It seems, therefore, that to whatever extent rattlesnake activities reach a low point in summer, the reason is to be sought in a lack of need for activity rather than uninterrupted lethal temperatures. By summer the mating season is over and the spring hunger to replace tissue and fat lost during hibernation has been satiated. Feeding intervals have now become matters of weeks if not months, and food may, indeed, often be secured in the mammal holes or rock crevices in which

both the snake and its prey have sought refuge. The rattler simply has nothing to do above ground and remains in some underground sanctuary at whatever level it finds the temperature affording the greatest comfort and metabolic well-being. This is not estivation in the sense of a period of suspended bodily functions, nor is it enforced by unbroken periods of high temperatures above ground.

It might be thought that the summer inactivity of rattlers is more apparent than real, for obviously they would be less frequently observed after becoming nocturnal in the summer as compared to their diurnal or crepuscular presence at other seasons. But studies of the sidewinder indicate that such is not the case. This snake is most easily collected if the hunter drives on black-top (asphaltic) pavements at night. It is found to be common in the spring but is scarce in the summer, even though the search may be made during the night hours after the ground and air temperatures have been reduced to a level quite comfortable to a sidewinder.

Whether snakes of other kinds in other areas estivate I do not know. Corkill (1949, p. 615) says snakes estivate in the Sudan. Prater (1933, p. 472; Fraser, 1936-37, p. 270; M. A. Smith, 1943, p. 305) believes that *Natrix stolata* of India estivates. This may be a dry-season rather than a temperature-induced estivation, since it ends with the breaking of the monsoon. It is analogous to the estivation of the slender salamander (*Batrachoseps*) during the long dry summers in California.

Volsøe (1944, p. 17), in discussing the activities of the European viper, points out that true estivation would involve a torpidity comparable to that of hibernation. To produce such a condition at relatively high temperatures would require a temperature-regulating mechanism that the snake does not have. He feels that the belief in estivation merely results from the increased nocturnality of the vipers. W. E. Taylor (1892b, p. 355) believes that rattlers become truly torpid in summer, but there is no evidence that their mere lack of activity can be so designated. Hopley (1882, p. 162) attributed estivation to the prairie rattlesnake. In all probability the difference of opinion regarding rattlesnake estivation is one of semantics rather than of fact. Certainly their activity above ground is greatly curtailed in the summer, especially in the daytime, but they would have no difficulty in becoming active instantly should conditions require.

#### EFFECTS OF HUMIDITY

It is probable that, next to temperature, humidity may be most important in controlling rattlesnake activity.

In coastal California, winter rains are the rule, and are coincident with cool weather, hence tending to inhibit snake activities. But in sections of Arizona, Sonora, and adjacent areas of the Southwest where summer is the season of rainfall, our experience seems to bear out the popular belief that snakes—rattlers included—are more active after the rains begin than before. It is probable that the rain has a sufficiently cooling effect in this hot season to make it feasible for the snakes to forego their nocturnal habits for a time, and in any case rain and clouds bring the temperature down nearer to the snake optimum. Also, they may sometimes be flooded out of their holes. Speaking of this area, Hrdlička (1908, p. 172) says that venomous snakes are more common in wet than dry weather, and Ramsey (1945, p. 23) observed that rattlesnakes were especially prevalent after summer showers. Ruthven (1907, p. 593), collecting in southeastern Arizona, found

that the western diamond rattler (*C. atrox*) was more frequently found on cloudy or foggy days, or after rains; and Ortenburger and Ortenburger (1926, p. 117) noted that this snake did not seem to mind a hard, beating rain, and made no effort to seek shelter, although bushes and holes were available nearby. Hilton (1947, p. 127) found reptiles more plentiful in Sonora after the first summer rain.

Speaking of *atrox* in Texas, J. D. Bankston of Mason, Texas, states: "They move around at night, or in early morning, or on a cloudy, showery day." Colonel M. L. Crimmins, who has kept statistics on the incidence of rattlesnake bite in the vicinity of San Antonio, Texas, advised me that such cases were likely to be brought to the hospital after heavy rains. They were fewer at times of prolonged dry spells. P. Bruce Centerwall, Tonto Basin, Arizona, wrote under date of June 29, 1945: "Right now, it having been dry for so long, snakes are not on the move very much. It should rain in the next couple weeks and start them going again."

Some of my correspondents in the intermountain area think rattlesnakes are most active prior to thunderstorms:

I have noted rattlers active at all times of the day and night; however, in normal summer weather, it is unusual to find one out and around other than between 4 P.M. and 9 P.M. On cool, rainy days, they may be out in the middle of the day. In muggy, humid weather, such as occurs just before thunderstorms, snakes are active all night long and until the sun grows warm the next day. *George W. Case, U. S. Forest Service, Saint Maries, Idaho.*

◇

Rattlesnakes are more active in hot, humid weather, although usually found in shady places. Just before thunderstorms begin seems to be a good time to run into rattlesnakes. *H. W. Parks, U. S. Forest Service, Warren, Idaho.*

◇

Rattlers are most active in the evening or just before lightning storms. Usually in the evening they are heading for water, or looking for prey found near water at that time of day. *E. J. Parker, U. S. Forest Service, Ukiah, Oreg.*

◇

I have noted that rattlesnakes are most active past the middle of the afternoon, or just before a rain. *Riley Millegan, Silver City, N. Mex.*

Curran and Kauffeld (1937, p. 62) reported that the southeastern pigmy rattlesnake (*S. m. barbouri*) comes out after heavy rainstorms, and Fitch (1949b, p. 89) says that the western pigmy rattler (*S. m. streckeri*) is most often found abroad after warm summer rains.

As is to be expected, rattlesnakes sometimes cool themselves by resting in the infrequent pools and seeps of the arid West:

On July 20, 1934, I found a medium-sized Great Basin rattler (*C. v. lutosus*) floating placidly in a tiny pool of a slow-seepage spring under an overhanging ledge of one of the drier and more barren draws of the eastern Peavine Mountain, northwest of Reno. On this particular occasion I slipped in under the ledge and drank my fill of water, before noticing the snake whose head was not more than eight inches from my face during the entire proceeding. As I drew back (it is necessary to crawl prone the last couple of feet to reach the spring) I noticed the snake. Only his head and a short portion of the neck were resting at the edge of the two-foot pool, the rest lying three-fourths submerged. I lay there and watched it for about 15 minutes, then went on my way, leaving the animal in my drinking water. All the while the snake made no movement, and I did not attempt to startle it. My impression was that the snake was enjoying the cool water, for it was a record hot day outside, and everything else was under cover. *Ira La Rivers, University of Nevada, Reno, Nev.*

The effect of rainfall in increasing activity seems to apply to many areas and to all kinds of snakes. Elliot (1934a, p. 506) was told by a professional snake catcher in England that snakes were particularly prevalent in July after rains. Fraser (1936-37, p. 270) says that the monsoon brings out snakes in India; Simson (1886, p. 239) said that the rains in eastern Bengal caused the snakes to seek shelter in human habitations; and Pitman (1938, p. 3) found snakes most plentiful in Uganda after periods of heavy rains. It might be thought that in tropical countries having a high annual precipitation, the snakes, many of semiaquatic kinds, would naturally be seen more often after rains. However, this certainly does not explain the situation in the Sonoran Desert, where only a few garter snakes are semiaquatic.

#### DIURNAL VARIATIONS IN ACTIVITY

I have discussed the seasonal effects on rattlesnake habits and shall now touch upon the diurnal effect. Necessarily the two are closely interrelated, yet an attempt to separate them will clarify the discussion. The snakes are somewhat more independent in choosing daily than seasonal periods of optimum temperatures, for they can take refuge underground against an unfavorable day, but not always against an unfavorable season, if they are to survive.

Their most obvious expedient, of course, is to become active at the time of day or night when the temperature conditions are nearest the optimum, and this is done to a certain extent. But it is evident that, other things being equal, most Nearctic rattlers prefer nocturnal to daylight activity, even though the temperature may be less favorable then. No doubt this is because the small mammals that constitute their principal food supply are also primarily nocturnal, although their choice may be partly induced as a protective measure against enemies. It is to be remembered that the rattlesnake's eyes are well adapted to night vision, and that the pit, as a high-temperature receptor, is probably more effective at night because of the greater temperature differential between the warm-blooded prey and the surrounding objects.

The following generalities are valid: Rattlers are more nocturnal in summer than in spring or fall; desert rattlesnakes are more nocturnal than those in more humid areas or where the brush cover is heavier; lowland rattlers are more nocturnal than montane individuals or species; and adult rattlesnakes are more nocturnal than juveniles. All of these trends are only partly the effect of temperature; equally important are food availability and requirements, protection from enemies, and the avoidance of direct sunlight (when more intense than desirable) and desiccation. That temperature alone is by no means the most important or controlling criterion is readily to be noted in the case of such desert species as the sidewinder (*C. cerastes*) and the Mojave rattler (*C. s. scutulatus*) both of which will be found active at night on the desert in seasons when the daylight hours would offer much better temperature conditions. The greatest surprise that awaits the person who believes the rattlesnake to be essentially a warm-weather or diurnal creature is experienced when he comes upon sidewinders and Mojave rattlers active at night on the desert with a bitterly cold wind blowing—a wind so strong one must lean against it in walking, while it cuts through a heavy overcoat to the accompaniment of whirling sand and debris.

With these variations in diurnal activity, incident to variations in temperature, humidity, seasons, altitude, brush cover, food supply, and other conditions, brief statements as to times of activity within the day, whether by my own correspondents or from published reports, would have no particular value unless all the associated conditions were also listed, and these are seldom available. Various correspondents have supplied data emphasizing activities at different periods: In the daytime, daybreak, morning, afternoon, evening, or night. However, these divergences of viewpoint are really not conflicting, for they pertain to different seasons, territories, altitudes, and species. But from my discussions of rattlesnake danger with such people as hunters, fishermen, campers, mountain climbers, and others making excursions into the wild, I am surprised at the extent of the belief that rattlesnakes are universally diurnal, or, under extreme circumstances only crepuscular, so that with darkness any danger vanishes. This has led to accidents in walking about a camp at night without the precautionary measure of a flashlight or even shoes. For this reason, I shall cite enough evidence to convince anyone that, regardless of the extent of their diurnal and crepuscular activities, rattlers certainly don't turn in for the night when darkness falls.

I have myself found the following southwestern species and subspecies active at night—meaning by “night,” after complete darkness: Western diamond (*C. atrox*), red diamond (*C. r. ruber*), Mojave (*C. s. scutulatus*), prairie (*C. v. viridis*), Arizona prairie (*C. v. nuntius*), Great Basin (*C. v. lutosus*), northern Pacific (*C. v. oreganus*), southern Pacific (*C. v. helleri*), southwestern speckled (*C. m. pyrrhus*), Panamint (*C. m. stephensi*), tiger (*C. tigris*), Mojave Desert sidewinder (*C. c. cerastes*), Colorado Desert sidewinder (*C. c. laterorepens*), and Sonoran Desert sidewinder (*C. c. cercobombus*). Some of these were observed up to midnight, and the only reason they were not found later was the cessation of my own activity, for other collectors have found them active all night in summer. In the desert, in the spring when the ground cools rapidly, activity is largely restricted to the early night hours.

I was told recently of a large diamondback (*C. adamanteus*) found by hunters active at night in January near Toledo, Charlton County, Georgia. *Francis Harper, Swarthmore, Pa.*



On three occasions, in the last ten years, I have seen rattlesnakes [*C. h. atricaudatus*] crossing the road at night. *T. S. Seely, U. S. Forest Service, Talladega, Ala.*



The rattlers here [*C. h. atricaudatus*] are mostly nocturnal, coming out about sundown, except in the late fall when they feed day and night to fatten up for hibernation. *J. M. Shevlin, Alexandria, La.*



Texas diamond rattlesnakes [*C. atrox*] travel mostly at night, though seen also during daytime. In hot weather they seek a cool shady place to rest in during daytime. *A. J. Kirn, Somerset, Texas.*



During hot weather rattlers are active almost entirely at night. *Dean M. Earl, U. S. Forest Service, Luna, N. Mex.*



In the Santa Cruz Valley of southern Arizona, the rattlers always come out at night and seem to frequent the bases of the low hills or river terraces. This observation is mainly made from the fact that so many were seen on hot summer nights on the road where it skirted one of these low mesas. *Louis R. Caywood, National Park Service, Santa Fe, N. Mex.*

Rattlesnakes [*C. v. viridis*] must move around a lot at night. For example, on a sultry night I remember hearing three rattle nearby at one time. *Fred A. Cook, U. S. Forest Service, Aspen, Colo.*

Rattlers don't seem to move about much in the heat of the day unless disturbed. I have seen them crossing the road in the car lights about midnight. *Charles G. Holzworth, Kremmling, Colo.*

In July, August, and September, the prairie rattlesnakes here [*C. v. viridis*] can be seen almost any time, on river trails; on hot nights you will contact as many as in the daytime. *John W. Warren, U. S. Forest Service, Hamilton, Mont.*

I have seen rattlesnakes [*C. v. lutosus*] traveling several hours after dark. *B. K. Crane, U. S. Forest Service, Austin, Nev.*

You are sure to find rattlers [*C. v. oreganus*] at any time of night in late May, June, July, and August, especially on very warm evenings or nights. *Marion E. Rose, Pateros, Wash.*

We find the rattlesnakes here [*C. v. oreganus*] to be most active in the evening after the sun has gone down during very warm weather. During the heat of the day they usually are found coiled up in the shade of bushes or among rocks. For a long time I was of the opinion that rattlesnakes did not travel after dark, but this belief was rudely dispelled one evening when one came up to the door of our guard station as we were sitting on the porch. *L. J. Cooper, U. S. Forest Service, Merlin, Oreg.*

Rattlers [*C. v. oreganus*] are most active during the late part of the day from about an hour before sundown until the evening starts to get cool. On warm nights they move around all night. *Bernie I. Leas, Fire Control Assistant, Platina, Calif.*

Two years ago while fire-proofing the highway, the crew killed a number of rattlers [*C. v. oreganus*] along the roadside between 8 o'clock and midnight. *George A. Fischer, U. S. Forest Service, Tulelake, Calif.*

Pacific rattlesnakes travel at night, for I have killed them crossing the roads in Solano County, especially roads bordering a stream or creek. *J. E. Hughes, Game Warden, Sacramento, Calif.*

I have found the majority of rattlers [*C. v. helleri*] between sunset and shortly after midnight. In the early hours of morning they become scarce and by daylight can rarely be seen. They are fond of seclusion and prefer privacy to anything else. *K. R. Halstead, San Bernardino, Calif.*

I have seen rattlesnakes [*C. v. oreganus*] quite active on hot moonlight nights in Colusa and Lake counties. *M. W. Durham, U. S. Forest Service, Pasadena, Calif.*

In most of the above quotations I have inserted, in brackets, the subspecies of rattlesnake to which each statement applies.

Some published accounts of the nocturnal activities of rattlesnakes are those of Ditmars (1936, p. 358) on the eastern diamond (*C. adamanteus*); Hudson (1942, p. 86) and McCauley (1945, p. 137) regarding the timber rattlesnake (*C. h. horridus*); Cook (1943, p. 50) on the southeastern pigmy rattler (*S. m. barbouri*); Fautin (1946, p. 294) on the Great Basin rattler (*C. v. lutosus*); and Fitch and Glading (1947, p. 107) and Fitch (1949a, p. 517) on the northern Pacific rattlesnake (*C. v. oreganus*).

Col. M. L. Crimmins reports that the mottled rock rattler (*C. l. lepidus*) comes out at sundown. Kauffeld (1934b, p. 609) noted that banded rock rattlers (*C. l. klauberi*) and Arizona twin-spotted rattlers (*C. p. pricei*) in captivity were most active in the late afternoon and at night. It is a common observation that captive rattlesnakes of many species roam about their cages more at night than in the daytime. Some of my own field observations and those of my associates on rattlesnakes at night are given in the following publications: Klauber, 1931a, p. 359 (*C. tigris*); 1932b, p. 128 (*C. c. cerastes*); 1936a, p. 168 (*C. m. stephensi*); 1939a, p. 26 (declining activity as the desert cools); 1939a, pp. 46, 48 (hours of night activity); 1944, p. 109 (*C. cerastes*).

Unfortunate, from the standpoint of public safety, are published statements that rattlers are rarely, if ever, nocturnal (e.g., Burton, 1861, p. 194; Anon., 1872b, p. 642; Rollinson, 1948, p. 232).

Whether the moon has any particular effect on the night activities of rattlesnakes is not known. As to desert reptiles in general, such evidence as has been accumulated indicates that they probably prefer dark nights and are less active under conditions of strong moonlight (Klauber, 1939a, p. 50).

It is not my intention in citing these instances of the night activities of rattlesnakes to give the idea that they are exclusively or even essentially nocturnal. I might have quoted, from many correspondents and published accounts, statements regarding their being found abroad at all times of the day, from early morning to late evening, for much depends on the season and temperature. As might be expected, reports from high altitudes indicate little night activity, although there is evident a tendency to become crepuscular in summer. My reason for stressing the night phase is because it seems to be little known to the public generally. And, of course, it is far from true that rattlers are the only snakes abroad at night; on the contrary, it is probable that most snakes become nocturnal when the daytime temperatures are too high. And some genera, particularly such desert forms as *Chionactis*, *Phyllorhynchus*, and *Chilomeniscus*, are almost exclusively nocturnal regardless of thermal conditions. Simson (1886, p. 242) mentions the fact that in India the cobra is mostly nocturnal.

It is probable that the rattlesnakes whose activities are least nocturnal are those that inhabit mountains at altitudes where day temperatures are seldom uncomfortably high, and night temperatures generally below 60° F. Dr. F. A. Shannon advised me that the little Tancitaran dusky rattlers (*C. pusillus*) and central-plateau dusky rattlers (*C. t. triseriatus*) on Cerro Tancítaro, Michoacán, Mexico, seldom came out in abundance before late morning. (This was in June and July). Then the noon rains would drive them to cover, after which they would come out in greater force, when clearing skies permitted a heat maximum for the day, which rarely exceeded 68° F. Thorough hunting at night failed to produce any specimens. This was at altitudes of from 5,500 to 10,600 feet.

J. T. Marshall, Jr., observed that *C. willardi*, another montane species, is primarily active in daylight. It does not avoid the direct morning sun in summer.

#### THE BASKING RANGE

In the process of determining the temperature-activity interrelationship of rattlesnakes, some distinction should be made between mere basking in the sun and true

activity—that is, the pursuit of some definite objective other than warmth. When ground and air temperatures are such as to result in a suboptimum body temperature, snakes often increase their comfort and well-being by basking in direct sunlight, thus securing the increased warmth of direct radiation. This is the basking range as defined by Cowles and Bogert (1944, p. 277). Basking is likely to be indulged in whenever the air temperature is below about 75° F., the ground is cool, and the sun is shining. Rattlesnakes probably seldom bask when air temperatures are below 55° F., unless the surface of the ground has already been warmed well above this level by the sun's rays. The combination of ground, air, and radiation conditions must be such as to cause an increase in the snake's temperature toward 75° F., or above, before the snake will seek to bask. In this connection, wind conditions—or the availability of a sunlit nook protected from the wind—are important, since a cool breeze will cause a greater loss of heat through convection than that accumulated from impinging radiation or from conduction. It is clear that a mere record of ground and air temperatures will not suffice to define the basking range; the important condition is that the effect of the radiation must sufficiently overcompensate for the other heat losses so that the temperature of the snake will be brought upward toward a more comfortable and beneficial level than would otherwise be possible. Should the temperature rise above this level, the snake will withdraw into the shade.

Taking advantage of basking is important in increasing a species' geographic range, for it lengthens the season during which body temperatures adequate to such processes as digestion and gestation are available. Since a snake can digest its food only when the exterior temperature flux produces an adequate internal temperature, basking may be likened to cud-chewing by a cow—an aid to digestion. Bogert (1949, pp. 196, 199, 205) has discussed the importance of basking to lizards.

Of all the examples of basking, the most conspicuous are those wherein the rattlers are found lying around their dens in the last sunny days of the fall or the first of spring. These habits have been discussed under hibernation.

Some typical examples of basking under extreme weather conditions are the following:

In western Arkansas, I found two rattlesnakes sunning themselves on rocks on the south side of a mountain during the month of February, with about a half an inch of snow on the ground; however, there was no snow in the immediate vicinity of the snakes, as it had melted off the rocks. *J. P. Brown, U. S. Forest Service, Walhalla, S. C.*



I caught a large Mojave rattler today at one P.M. while he was having a sun bath. It was a cold day for this place, and there was ice last night. *M. E. Spivey, Date Creek, Ariz.*

Basking is not restricted to times of severe weather conditions, such as early spring or late fall, but may be utilized for brief periods at some time of day at any season when temperature conditions are suboptimum and the sun is shining. Thus in the late spring and at higher elevations in the summer, rattlesnakes will be found basking in the sun in the early morning, since the later midday air and ground temperatures will be above the optimum. This is highly characteristic of sidewinders in the desert. Collectors, following along their tracks made the night before, will usually find them coiled in a self-made depression, in the sun, but always near some bush or mammal hole in which they can seek refuge as soon as the air and ground temperatures attain an unpleasant level.

## OTHER TEMPERATURE-CONTROL EXPEDIENTS

In addition to attempting the adjustment of their activities to periods of favorable seasonal and diurnal temperatures, rattlers adopt various expedients to secure the advantages of favorable differences in microclimate.

One of the simplest of these methods is to take advantage of temperature differences within a narrow space. Rattlesnakes make a practice of lying in the edge of a patch of shade, where, by varying the relative amounts of shade and sun upon the body, the snake can attain any temperature between the cool of the shade and the maximum produced by the full solar radiation. A movement from full sun in the morning to full shade at noon, with a return to basking in the afternoon is a common maneuver; T. E. B. Pope (1925a, p. 19) and McCauley (1945, p. 137) are among the authors mentioning this routine.

Rattlers have another way of averaging temperatures when one position is too high and the other too low for comfort. In the morning in the desert, the ground is often quite cool only an inch below the surface; for sand, with its air-filled interstices, is a relatively poor conductor of heat. Sidewinders have a way of bedding themselves down by manipulating their coiled bodies until their dorsal surfaces are level with the sand (fig. 7:4). When the snake is in this position the dorsum is heated by the sun's rays while the ventrum is cooled by the substratum. This explains the occasional finding of sidewinders exposed to the sun in the morning as mentioned by Camp (1916, p. 535), although, as Mosauer (1936a, p. 63) has pointed out, they are more frequently at least partly in the shade, to which they must shortly retire in any case. Such a sidewinder movement is so well known as even to be mentioned in fiction (Wilson, 1945, p. 70).

Several temperature-adjustment schemes are available to lizards but not to snakes, among these being the elevation of the body by standing with the legs stiffened to avoid contact with and conduction from the ground. Another expedient that the lizards can employ to control the absorption of radiation is to vary the body hue and therefore reflectivity. These color changes have long been known in the lizards—the best recent exposition is that of Atsatt (1939, p. 237)—but it is not so well known (and, in fact, has been denied) that rattlesnakes have some power of color change. I have observed it in the southern Pacific rattlesnake (*C. v. helleri*), the Arizona black rattler (*C. v. cerberus*), and the sidewinder (*C. c. laterorepens*) (Klauber, 1931b, p. 46). It has been shown by Rahn (1941, p. 228) that there is a pituitary regulation of the epidermal melanophores in the prairie rattlesnake (*C. v. viridis*) and that the pattern can be permanently lightened by excision of the pituitary. This would seem to verify the existence of some natural color-control in snakes, for a somewhat similar mechanism has been known to be present in the lizards, whose color variations are so marked. Kauffeld (1943a, p. 349) believes that rattlers gradually become lighter in captivity; this may be true in some cases, or it may be only an ordinary manifestation of age, for in most rattlesnake species the young are darker than the adults.

Of course, the principal means of temperature regulation available to rattlesnakes, when the external temperature is above the optimum, is to seek refuge in a mammal hole or a rock crevice. Dr. R. B. Cowles has shown by elaborate experiments carried on in the vicinity of Indio, California, that the degree of control is

much more accurately exercised to attain a particular optimum temperature than had previously been supposed. For, as experiments with sidewinders (*C. c. laterorepens*) proved, this was no simple matter of exchanging a dangerous temperature on the surface for an endurable one below ground. On the contrary, the snake took up whatever position—between partial exposure at the mouth of the burrow to maximum depth at the bottom—that would produce the most comfortable temperature, which, for this species of snake, proved to be between 31° and 32° C. (88° and 89½° F.) with an average of 31.4° C. (88½° F.). As the surface temperature conditions varied, the snake changed its position in the burrow to whatever location would maintain this body temperature. The results of this control secured almost as constant a body temperature as that produced by the internal control available to mammals. However, only at certain seasons are the conditions essential to this type of control available—a supraoptimum temperature at the surface at the entrance to the burrow and a suboptimum temperature at the bottom, with suitable resting places at all points between."

Since the advent of black-top pavements in our southwestern deserts, rattlers and other snakes have been observed warming themselves at night on these roads, after the desert air and ground temperatures have fallen below the preferred level. The storage of heat in the pavement is considerable. This is one of the reasons why night-driving on desert roads is so successful as a means of collecting snakes. Sometimes the snakes are moving when seen, but often they are stationary, or, in the case of sidewinders, coiled in their resting positions.

At Montezuma Castle I have seen a number of rattlers lying perfectly motionless, stretched out on the oiled entrance-road at night. Presumably, the retained heat is pleasant to them at night. *Earl Jackson, National Park Service, Las Vegas, Nev.*

It is probable that under natural conditions rattlesnakes are seldom killed by heat. Although the warning zone of danger is relatively narrow, and the critical zone of muscular damage quite quickly attained by an exposed snake, only in the rare contingency of a snake being caught in a bare expanse of desert would the situation be likely to prove fatal. At times when diurnal temperatures reach these dangerous extremities, the rattlesnakes have largely become nocturnal; and while the early morning often finds them in the sun, it will usually be close to the shade of some bush. When surface temperatures attain dangerous extremes even in the shade, mammal burrows and rock crevices are sought. In the morning, rattlers are usually found near such refuges.

In comparison with other desert animals, snakes, especially rattlers, suffer from certain disadvantages that limit their ability to cope with high temperatures. Their relatively slow speed may be fatal where a faster animal, such as a lizard, could reach safety. Slow speed also prevents loss of heat by convection when the body temperature is higher than that of the air, for an undisturbed air film—the so-called skin effect—acts as an insulator. Again, the close contact of the body with the ground results in a rapid transference of heat from the soil to the body when the temperature gradient is in that direction, as it often is under dangerous conditions. Desert lizards are frequently observed with their bodies erected to the limit of their legs, to escape this conduction. Nor have the rattlers—not even the

<sup>a</sup> Woodbury and Hardy (1949, p. 181) have furnished interesting data on surface, compared with subterranean temperatures, of desert-tortoise dens in Utah.

sidewinder<sup>a</sup>—an ability to bury themselves in sand quickly as have some lizards, such as the fringe-toed sand lizards (*Uma*) and the horned toads (*Phrynosoma*), or burrowing snakes like *Chilomeniscus*. Often the temperature fall below the surface is quite steep so that safe temperatures are reached only a few inches down. Snakes, with few exceptions that include no rattlesnakes, lack a black peritoneum, a protective device with which certain diurnal lizards are equipped (Klauber, 1939a, p. 75); however, this is more important as a selective wave-length screen than in reducing the total incident radiation. In these deficiencies, snakes—rattlers among them—suffer in comparison with their nearest relatives, the lizards. Bogert (1949, p. 195) has discussed behavioral thermoregulation in the lizards, as determined from field experiments in Florida.

Snakes are at a still greater disadvantage compared with the birds, and particularly the mammals, in having no special means for increasing skin evaporation, such as sweat glands, although, as indicated by Bogert and Cowles (1947, p. 1) they may possibly lose moisture through the skin. Their relatively small lung surfaces, together with limited surplus body fluids, greatly limit the possibility of temperature reduction through internal evaporation, of which the panting of dogs is the most familiar example. However, Bogert and Cowles (1947, p. 1) have shown that as the critical temperature is approached, snakes can lower their temperatures a few degrees by panting, although it may be doubted whether this protective expedient could be maintained for more than a few minutes, so limited is their moisture reserve. In fact, it has been noted by these authors (p. 30) that desert snakes lose moisture less rapidly than those restricted to moist habitats; thus it would appear that moisture conservation rather than cooling is of supreme importance. Were the surplus moisture of desert reptiles adequate, we would expect them to have developed a superior rather than a reduced capacity for evaporation through the skin, in order to profit from the cooling effect.

But despite these handicaps, the advent of high temperatures may be so readily foreseen, and may be so easily counteracted by the snake's going down a hole, that the death of a rattler from heat under natural conditions must, indeed, be a rare accident.

#### AREAL DIFFERENCES IN ACTIVITY

I have discussed the extreme temperatures that completely limit rattlesnake activities—the lethal maximum and minimum (using the terminology of Cowles and Bogert, 1944, p. 277), and the critical maximum and minimum, the latter the temperatures at which locomotion becomes disorganized or impossible. Between these lie levels of voluntary maximum and minimum temperatures. If the temperature goes above or below either of these, the snake will go underground for safety, even though, in the case of a voluntary minimum, a still lower temperature may be met there. The actual positions of these levels seem to vary

<sup>a</sup> The Saharan vipers cover themselves with sand more readily than the sidewinder, for they bury themselves with a lateral shaking motion that quickly takes them below the surface (Pawlowsky, 1927, p. 279; Mosauer, 1934, p. 59), whereas the sidewinder normally beds itself down only to a depth such that its back is flush with the sand surface. Occasionally drifting sand may cover it, and, according to Cowles, it may actually use the head to hook sand back over the body. But this is not as usual or intentional as is the case with the African snakes. However, even these depend on mammal holes for their principal refuges, for Anderson (1898, p. 332) states that the majority of specimens that he collected were dug out of holes presumably tenanted by rodents.

somewhat with the species and the ecological niche in which the animal lives, as well as the snake's hunger or mating proclivity. The necessities of food and reproduction, and the length of the growing season may force a snake in one area to remain active under conditions that would be avoided by temporary retirement in another. For example, the sidewinder, a rattlesnake which, despite its desert habitat, is probably as inured to low temperatures as any, is active in the higher, colder Mojave Desert at temperatures that it seems to avoid in the lower, warmer Colorado Desert. No doubt the shorter season of preferred temperatures in the Mojave requires this nocturnal snake to pursue its activities under more adverse conditions there, if it is to have a growing season long enough to persist at all. I have hunted extensively at night in both deserts and found 25 per cent of the sidewinders taken alive on the road at night in the Mojave at air temperatures (63° F. or lower) below those at which any Colorado Desert specimens were taken; and 75 per cent of the Mojave specimens were taken below a temperature level at which only 10½ per cent of the Colorado Desert snakes were found (Klauber, 1944, p. 111). I have, in fact, found sidewinders in the Mojave active at air temperatures—probably slightly below 60° F., but unfortunately before accurate records were kept—lower than that experienced with any other rattlesnake (Klauber, 1932b, p. 128; 1939a, pp. 14, 49), although I have found the Mojave rattler (*C. s. scutulatus*) active at 63° F., and the red diamond (*C. r. ruber*) at 64° F. (p. 50). It should be said that cold, strong winds are frequent in the spring nights on the desert; the ground surface cools rapidly and there is little or no protection by shrubs, so that the body temperatures of the snakes met under these conditions do not differ from the air temperatures.

The relative degrees of nocturnality among the rattlesnakes apparently depend both on the species and the ecological conditions in which it lives. One may start with the generality that Nearctic (United States) rattlesnakes are diurnal or crepuscular in the spring and fall, and nocturnal in summer. But it is further evident that those species that are wholly or largely restricted to deserts are more nocturnal than those inhabiting other kinds of territory; that is, they are not only more nocturnal to the extent that their hotter territory requires, but they are apparently nocturnal under spring and autumn thermal conditions when the daytime temperatures are nearer the optimum than those at night, and under conditions that would cause the nondesert reptiles to be diurnal. This is the case with such desert species as the sidewinder (*C. cerastes*), the western diamond (*C. atrox*), the Mojave rattler (*C. s. scutulatus*), and the tiger rattler (*C. tigris*). Other rattlesnakes, particularly those that range through areas of diverse ecological characters, seem to be more responsive to the particular thermal conditions that they must meet from day to day—that is, they are likely to be diurnal when the nights are cool, and nocturnal when the days are hot. For this reason, it is not at all unusual to observe temperature-activity differences within species; for example, the red diamond (*C. r. ruber*) and the southwestern speckled rattler (*C. m. pyrrhus*) are more often found out at night in the desert foothills than in coastal southern California, and the northern Pacific rattler (*C. v. oreganus*) is more nocturnal in the San Joaquin Valley than in the Coast Range or the Sierra Nevada. However, although able to fit them-

selves to the local necessities, they are less consistently nocturnal than the truly desert forms. This greater degree of nocturnality of desert species may result from the thinner desert cover that affords less protection against enemies and excessive solar radiation, or from the more pronounced nocturnality of the desert prey.

Admittedly these conclusions are not entirely objective. The difficulty of finding rattlers at night, compared with the daytime, discriminates against the night observations. Only figures based on the live snakes found by driving on black-top roads day and night are truly comparative, and even these are somewhat affected by the degree to which the snakes may avoid the open spaces of roads in the daytime or seek the warmth of the pavement as the desert cools at night. I have given some comparative figures elsewhere (Klauber, 1939a, p. 38).

#### EFFECTS OF FOOD SUPPLY ON TEMPORAL ACTIVITY

Conditions of food supply seem to have some, but not an overriding, effect on the seasonal or daily activities of rattlesnakes. There should not be inferred from this statement a lack of importance of the food supply, but rather that the prey are so largely affected by the same temporal conditions as the rattlesnakes that they are naturally active at the same time as the snakes, which, therefore, need not modify their normal habits to accommodate themselves to those of the prey.

Rattlesnakes of the smaller species and the young of the larger forms subsist to a considerable extent on lizards. These, being ectothermic like the predators, are likely to experience similar limitations in activity through the effects of temperature. However, in general, lizards are more diurnal than rattlers, which may be one of the reasons why young rattlers are more diurnal than adults.

With respect to small mammals, especially rodents and lagomorphs, although these can withstand a much wider range of external temperatures than the snakes, and are found abroad at times when the snakes have been forced into seclusion, yet their activities are also largely crepuscular or nocturnal, so that the rattler need not change its schedule to secure its food. Nevertheless, it is probable that in some desert areas, the Mojave Desert in particular, the rattlesnakes are more nocturnal in the spring than would otherwise be the case, the night temperature in that season being a full 20° F. or more below the snake optimum. The rodents, not being seriously affected by the night temperatures, are nocturnal as a protection against diurnal predators, hawks especially, and the rattlers must follow suit.

It may be pointed out that both lizards and mammals seek refuge in holes, and without doubt many a capture is made by a rattler without stirring from its own hiding place.

Seasonally, somewhat the same favorable conditions exist for the predators. The annual crop of young lizards is born at the same time as the newly born rattlers that require them for food. Fitch (1949a, p. 549) has pointed out how favorably the seasonal activities of the ground squirrels on the San Joaquin Experimental Range fit with those of the rattlers that prey on them, to the advantage of the snakes. The ground squirrels are diurnal; the young are born in the spring and are of just the right size to furnish a full meal for adult rattlers at the time the latter are diurnal and at the seasonal peak of their activity.

## CLIMATE AND SIZE

Cowles (1945, p. 563; see also Bogert, 1949, p. 201) has pointed out that reptiles tend to be larger in warmer and smaller in colder climates. Among the rattlers this is more evident altitudinally than latitudinally, for most mountain species are small, and species that range through a wide belt from lowlands to mountains are represented by smaller individuals at the higher elevations. But with respect to latitudes, the size variation is neither so evident nor consistent. Generically speaking, the rule does hold; the largest species (*adamanteus*, *atrox*, *durissus*, and *basiliscus*) are found in the warmer areas of the United States and Mexico. Intraspecifically, the theory sometimes holds and sometimes does not, for food supply may prove of overbalancing importance. The prairie rattler (*C. v. viridis*) reaches its greatest size in the north; at its southwestern limit, in the barren Painted Desert, it is represented by a stunted form, the Arizona prairie rattler (*C. v. nuntius*), and in the intermountain area by the midget faded rattler (*C. v. decolor*). The western massasauga (*S. c. tergeminus*) is smaller than its northern relative, the eastern massasauga (*S. c. catenatus*). The northern Pacific rattlesnake (*C. v. oreganus*) seems to reach as large a size in Washington as in central California. On the other hand, the canebrake rattler (*C. h. atricaudatus*) is larger than its northern relative, the timber rattler (*C. h. horridus*). Similarly, the southern sidewinder (*C. c. laterorepens*) is larger than the northern (*C. c. cerastes*).

Stradling (1881, p. 148) claimed that British snakes, when removed to the tropics, grew to a larger size than at home. We have not found this to be the case at the San Diego Zoo, where many kinds of snakes are kept under ecological conditions assumed to be more favorable than their natural habitats.

## DEFENSIVE AND WARNING BEHAVIOR

As I have discussed in chapter 15, rattlesnakes have many kinds of enemies. Escape from these is one of the three most important requirements necessitating definite action upon the part of the snakes if they are to survive, the others being the pursuit of food and mates. Naturally, the reaction of a rattlesnake to the threat of an enemy depends largely on the character of the enemy and the accessibility of a refuge, as well as on the disposition of the rattlesnake. But, in general, there are three successive phases of defense: an endeavor to avoid detection through quiescence and protective coloration—the so-called method of procrypsis; an endeavor to escape by flight; and finally, if these fail, an active defense by coiling, threatening, and even striking. This last resort may be quite spectacular, and is the particular rattlesnake attitude upon which its sinister reputation is largely based.

## DISPOSITION AND TEMPERAMENT

Since a rattler's response to an exterior threat is by no means stereotyped, but depends on both the species of snake and its individual temperament, it will be desirable, first, to touch on some of the factors that affect the nature of the snake's reaction to intrusion.

It hardly needs to be said that the actions of rattlesnakes in defense can be judged objectively only by those who have had experience with them and are not unduly frightened by their threatening attitudes. The uninitiated are likely to be so startled that they see a violent attack even in a snake retreating toward some hiding place.

There are undoubtedly species differences in rattlesnake temperaments, for some are more nervous and excitable than others. They show this by throwing themselves into a striking coil more readily and quickly—they are “on the prod,” to use an expressive Western phrase. If kept in captivity, such species retain a menacing demeanor longer than others, although almost all rattlers eventually become inured to the presence of human beings.

At the top of the list of rattlers quick to anger, I should put the western diamondback (*C. atrox*), followed closely by the eastern diamondback (*C. adamanteus*), and then by several of the subspecies of the speckled rattlesnake (*C. mitchelli*). At the other end of the scale would be a notably peaceful rattler, the red diamond (*C. r. ruber*), a surprisingly mild-mannered snake in view of its close relationship to the western diamond.

Of course, all observers do not agree on the relative placing of the several species when graded as to temperament, for it is inevitable that their conclusions should be affected by their own field experiences with individual snakes. The following summaries, in an alphabetical order of species technical names rather than in an order having any reference to a scale of temperament, give some indication of species variations. Although differences of opinion are expressed by the correspondents quoted, some general agreement is evident.

*Eastern Diamond Rattlesnake (C. adamanteus).*—It is generally agreed that the eastern diamondback is one rattlesnake that is ever ready to defend itself, and will often stand its ground against an adversary. Many captive specimens remain intractable over long periods. Ross Allen of Silver Springs, Florida, who has handled many thousands of these snakes, both in the wild and in captivity, has this to say about their characteristics:

Comparing the diamondback (*C. adamanteus*) with other rattlesnakes I have handled, I find it, on the average, to be the most dangerous and most persistent striker of all. The western diamond (*C. atrox*) is the only close second. I have seen diamondbacks that would continue to rattle and strike at me dozens of times each day for a month. Like other snakes, their temperaments and reactions vary, according to the snake and conditions.

If a diamondback has a chance to crawl away respectably, and hide from an intruder, he will do so; but, if approached, certain individuals will coil and rattle and blow and strike viciously. I have never known the diamondback to attack, but have seen them strike with such force as to slide forward. I have seen diamondbacks, after striking in vain and becoming discouraged, crawl away, nevertheless assuming a defensive position as they crawled backwards or sideways into the brush. I can safely say that the eastern diamondback rattlesnake, as a general rule, will stand his ground and fight rather than retreat or escape.

Another collector states:

There seems to be a great deal to be said both pro and con as to the aggressiveness of *C. adamanteus*. Of all that I have handled and caught, I have never had one attack deliberately. Most of them have beat a slow, backward retreat for cover, while at the same time poised in a most threatening defensive attitude. Others have tried to remain unnoticed

by flattening quietly, while still others have made a "bee-line" for cover as would a common blacksnake. I do not regard the diamondback as being actually aggressive at all. *John S. C. Boswell, Alexandria, Va.*

Haltom (1931, p. 100) says that *adamanteus* will not retreat at approaching danger, but Schrenkeisen (1930, p. 68) mentions several incidents in which it was not aggressive.

Carr (1940, p. 95) remarks of the eastern diamondback:

Its temperament is somewhat maligned by popular report. There seems to be a great individual variation in disposition; on a very few occasions I have heard diamondbacks rattle in apparent rage at my presence when they were concealed in palmettos 20 or 30 feet away. Much more often, however, they permit one to approach within 2 or 3 feet before becoming agitated.

*Western Diamond Rattlesnake (C. atrox).*—Most of those who have had experience with many species of rattlesnakes, alike in the field and in captivity, agree that the western diamond is the most temperamental and aggressive of the rattlers found in the United States. In the wild, it is ever ready to throw itself into its striking coil and to dispute the way with a trespasser; and in captivity many specimens maintain a fighting attitude for a long time. This is a dangerous rattlesnake, quick to anger, and resolute in defense; one whose threatening demeanor when aroused is backed by a hair-trigger readiness to strike.

Quite consistently, I find *atrox* far more argumentative and hostile than *molossus*. Only a little annoyance, after its initial attempt at escape has occurred, will usually stir *atrox* to hostility, although not many in my experience get angry enough to make lunges at their persecutor, even when teased with a stick. Of course, when one is injured, it is much more likely to strike. *Earl Jackson, National Park Service, Las Vegas, Nev.*

Werler (1950, p. 32) says of the western diamondback:

It has an unusually furious disposition and if threatened with danger or sufficiently annoyed, will vigorously defend itself instead of seeking immediate escape.

*Mexican West-Coast Rattlesnake (C. b. basiliscus).*—This rattlesnake tames quickly in captivity, as we have found at the San Diego Zoo, and as Mrs. Wiley reported (1930, p. 100).

*Sidewinder (C. cerastes).*—All through the Southwestern deserts, the sidewinder has the popular reputation of being particularly malignant (Gibson, 1940, p. 25; Blackford, 1946, p. 10), but I think this is largely the result of the romance that attaches to this queer little desert rattler, characterized by so fantastic a method of crawling. Whether in the field or at the zoo, I have found it an average rattler in disposition, neither especially pugnacious nor tranquil.

*Central American Rattlesnake (C. d. durissus).*—March (1928, p. 58; 1933, p. 72) thought this a calmer and less excitable rattlesnake than *adamanteus* and *atrox*. However, he also reported it to be a sinister and insolent snake, standing its ground when approached, and more aggressive, if attacked, than most Nearctic rattlers. He called it, in its method of defense, the most spectacular venomous snake in the New World. (Fig. 7:5 shows its threatening posture.) The South American subspecies (*C. d. terrificus*) is said to be of similar temperament.

*Timber Rattlesnake* (*C. h. horridus*).—The timber rattlesnake and its relative the canebrake (*C. h. atricaudatus*) are said to be relatively mild-mannered (Ditmars, 1907, p. 444; 1935, p. 33; 1936, p. 369; Wiley, 1930, p. 103; Schmidt and Davis, 1941, p. 301; Hudson, 1942, p. 87; Cook, 1943, p. 53; Breckenridge, 1944, p. 156; McCauley, 1945, p. 137). Ditmars (1936, p. 369) thought that the timber rattlesnake preferred retreat to combat, and, though rattling harshly when disturbed, would generally glide away, sounding its warning note as it went. But, if cornered, it would fight bravely.

*Small-Headed Rattlesnake* (*C. intermedius*).—I was advised by R. W. Axtell that the subspecies *C. i. omiltemanus*, because of the high altitudes where it occurs, is almost entirely diurnal, and, in fact, is usually out in the sun. Those found basking were very nervous and would coil and strike upon the least provocation.

*Rock Rattlesnake* (*C. lepidus*).—Of the eastern form—the mottled rock rattler (*C. l. lepidus*)—Werler (1950, p. 32) says:

It has a quiet disposition and if alarmed will immediately retreat within the masses of jumbled rock which are its home.

J. T. Wright of Tucson, Arizona, has advised me that the western subspecies—the banded rock rattlesnake (*C. l. klauberi*)—is a timid and peaceful snake. Kaufeld (1943a, p. 350) judged it to be timid but quite irritable—even frenzied—at times. Woodin (1953, p. 294) remarks that it evinces curiosity, since it does not escape so deep into the rock slides as it might for its own protection, preferring to stay where it can watch an intruder. L. H. Cook reported that snakes of this subspecies retreated when discovered, but rattled as they went.

*Speckled Rattlesnake* (*C. mitchelli*).—I have always found the various subspecies of the speckled rattler—except *C. m. stephensi*—to be rather nervous and pugnacious, more so than *viridis* and its subspecies.

Charles H. Lowe, Jr., thus reports his experiences with the stunted snakes (*C. m. muertensis*) on El Muerto Island:

The rattlesnakes (all nine) showed vicious dispositions. They rattled continuously from the moment they saw or sensed someone approaching, and continued to do so for a considerable time after being put in sacks. When touched, they thrashed their bodies about wildly. One snake bit the dirt three or four times in rage when held down by the neck. Another thrashed so violently and suddenly, after being picked up by the neck, that he threw himself right out of my grasp and onto the ground. Their vigorous actions, when within close proximity, lead one to believe that they have or have had some important enemy, perhaps a bird of prey. Ospreys and duck hawks live on the island.

The late Mrs. Grace O. Wiley thought the speckled rattler unusually gentle, but this may have been because the specimens she discussed in the following communication of some 25 years ago had already been in captivity for some little time when sent her:

*C. mitchelli*<sup>10</sup> excels any rattlers of my experience in gentleness. One hour after I got your rattlers I was stroking them with my hand and they were liking it. I wouldn't have dared to do this with newly captured *C. atrox*. One *mitchelli* humps its back as I stroke it. It will climb on my shoulder, arrange itself in a comfortable position (sometimes around my neck) and remain thus for half an hour. I can walk around and the snake never becomes frightened.

<sup>10</sup> Actually the subspecies *C. m. pyrrhus*.

With regard to the disposition of the Panamint rattler (*C. m. stephensi*), Wilbur Doudna, then of Boulder City, Nevada, wrote me:

With one exception, I have found these rattlesnakes mild-mannered. This exception was one on a trail high up on Tin Mountain in the Death Valley country. It was late at night, probably ten o'clock, and I was feeling my way along the trail trying to get back into camp, when the reptile sounded off at my feet. It seemed very angry, and never stopped rattling for an instant. In the darkness I could see it only as a darker blur on the ground. It gave ground slowly and only after much activity on my part. We managed to circle around it off the trail, leaving it in possession. In contrast to that, the largest Panamint rattler I have ever seen was at Gold Belt Spring in the same general region. I teased and abused this one unmercifully for half an hour, trying to rouse it to anger without success. I couldn't get a rattle or a strike out of it. It seemed to be normal in every way; it was in good condition and the weather was warm, so it was not sluggish because of temperature. The point I wish to make is that I have found this species unusually gentle in nearly all of my contacts with it.

I agree that *stephensi* is less excitable than *pyrrhus*, with which I have had a considerable field experience. The latter, when one comes upon it, will usually rise almost at once into a threatening coil and will stand its ground.

*Northern Black-Tailed Rattlesnake* (*C. m. molossus*).—At the San Diego Zoo we have not found this rattler conspicuously different from others. Taylor (1936, p. 497) reports one that did not rattle when approached. Schmidt and Smith (1944, p. 94) found it more inoffensive than the western diamond. J. T. Wright of Tucson, Arizona, writes:

The black-tailed rattlesnake has a reputation for aggressiveness, but several years of association with it in the field seem to me to prove the opposite.

Werler (1950, p. 33) also comments on the fact that some observers consider the blacktail irritable, whereas others claim that it is quiet and docile.

*Arizona Twin-Spotted Rattlesnake* (*C. p. pricei*).—L. H. Cook collected a number of these little rattlesnakes in the Chiricahua Mountains, Arizona. He said they rattled when discovered, and continued rattling as they sought cover. The rattles are so tiny they were barely audible. Kauffeld (1943a, p. 353) found *pricei* calm, much less nervous than *klauberi*.

*Red Diamond Rattlesnake* (*C. r. ruber*).—This handsome California rattlesnake, although a close relative of the western diamond, is conspicuously different in temperament, for it is probably the mildest-mannered of all rattlesnakes. If not roughly treated, it can often be caught without its making any attempt to bite, or even to sound the rattle. In captivity it quickly settles down to a peaceful and lethargic existence.

*San Lucan Diamond Rattlesnake* (*C. r. lucasensis*).—This snake is intermediate between *atrox* and *ruber* in many characteristics, and this is true also of disposition, although it leans more toward the peaceful *ruber*.

Veatch, as long ago as 1869 (p. 151), reported that the little Cedros Island diamond rattler (*C. exsul*) was, like its large mainland relative, *ruber*, of a mild character, difficult to provoke.

*Mojave Rattlesnake* (*C. s. scutulatus*).—This desert species, although long confused with the western diamond (*C. atrox*), is more peaceful in disposition. Some of the conflicting reports on western diamonds arise from confusion with this rattler. Because of its greenish color, *scutulatus* has also been confused with the blacktail. I have often collected it at night in the Mojave Desert and found that it usually endeavored to escape and only made a stand when prevented from reaching a refuge. L. H. Cook reported that Arizona specimens rattled only when annoyed.

*Tiger Rattlesnake* (*C. tigris*).—Such tiger rattlers as we have had in captivity quickly became lethargic. Schmidt and Davis (1941, p. 306) state that this is a relatively inoffensive rattler, not prone to rattle or strike.

*Tortuga Island Diamondback* (*C. tortugensis*).—This island form is less excitable and nervous than its mainland relative, the western diamond (*C. atrox*). Van Denburgh (1922, vol. 2, p. 919) said they would rattle vigorously when approached.

*Dusky Rattlesnake* (*C. triseriatus*).—According to Davis and Smith (1953, p. 142) this little rattlesnake is rather docile; specimens made no attempt to strike when captured. Dr. F. A. Shannon, on Cerro Tancitaro, found them alert, quickly escaping under rocks when approached.

*Aruba Island Rattlesnake* (*C. unicolor*).—This island rattler, although ready enough to defend itself, does not have the assurance characteristic of *durissus* and its mainland subspecies.

*Western Rattlesnake* (*C. viridis*).—The several subspecies of the western rattlesnake—the prairie (*C. v. viridis*), Great Basin (*C. v. lutosus*), northern Pacific (*C. v. oreganus*), southern Pacific (*C. v. helleri*), Arizona black (*C. v. cerberus*), Grand Canyon (*C. v. abyssus*), midget faded (*C. v. decolor*), and Arizona prairie rattlesnake (*C. v. nuntius*)—are much alike in temperament, and may be said to represent the rattlesnake mode in this characteristic, for they are neither particularly disputatious nor lethargic. Their reactions usually depend on the conditions under which they are discovered. Although they generally try to escape, they will put up a good fight if cornered or teased.

Of the prairie rattlesnake in the field, Hudson (1942, p. 88) reports that some individuals rattled furiously when disturbed, yet others failed to do so even when tormented, for they struck savagely without rattling.

I shall always remember the Grand Canyon rattlesnake (*C. v. abyssus*) as a snake of more or less even temperament. While I have met a few individuals that demonstrated a certain amount of viciousness, for the most part they were easy to handle. One incident that took place in Nankoweap Canyon, a branch of Grand Canyon, illustrates pretty well how prone this reptile is to avoid trouble. I was camping in the bottom of the canyon late one summer. Early one morning, while preparing breakfast, I went down to the creek to get a drink. Lacking any drinking cup, I knelt down by the stream to drink directly from the stream. In so doing I put my hand upon a large rock at the side of the stream, lowered my face to the water, and had an enjoyable drink. However, as I finished I was chilled considerably by looking back under my chest and noting one of these rattlers coiled there, with his head approximately 8 to 12 inches from my chin. You may be sure that I moved very cautiously in raising my head up out of harm's way, and just as cautiously in removing my body out of

range of the snake. During all this time, the only action that I saw in the snake was the questioning attitude of his flicking tongue. Obviously he was not at all angered at my presence and was apparently only curious to know what it was that had disturbed him. There was no warning given at any time; certainly there was no attempt made to strike. After my nerves had settled a bit, I teased this rattler to see what he would do. His only reaction was to try to get under the rock by which he was coiled. *Russell K. Grater, Park Naturalist, Rocky Mountain National Park, Estes Park, Colo.*

The southern Pacific rattler (*C. v. helleri*), is a rather nervous snake, easily roused to defend itself. This is particularly evident when it is contrasted with the placid red diamond (*C. r. ruber*), with which it shares much of its range. Grinnell and Grinnell (1907, p. 50) have reported a number of field experiences with this subspecies.

*Ridge-Nosed Rattlesnake* (*C. willardi*).—Woodin (1953, p. 295) found two specimens of the Arizona subspecies (*C. w. willardi*) that made no attempt to escape, and offered little resistance to capture. Stebbins (1954, p. 484) says *willardi* is prone to turn and bite without coiling.

*Massasauga* (*S. catenatus*).—Ruthven, Thompson, and Gaige (1928, p. 131) found the northern subspecies a sluggish snake, slow to bite, and one that usually sounded its rattle before striking. H. M. Smith (1950, p. 298) reported it more docile than most other rattlers. Woodin (1953, p. 294) met one of the southern subspecies (*S. c. tergeminus*) that was nervous and irritable; but Werler (1950, p. 31) considers this one of the most placid of rattlers, little inclined to use its rattle or to threaten.

*Pigmy Rattlesnake* (*S. miliarius*).—Ditmars (1936, p. 344) says, with reference to the Carolina subspecies (*S. m. miliarius*), that when annoyed this little snake will throw its body into a fighting coil, sound its rattle, and give vent to its anger by vicious jabs in the direction of the disturbance. Allen and Neill (1950b, p. 10) state that the southeastern subspecies (*S. m. barbouri*) has a fiery disposition. Werler (1950, p. 31) says that the western subspecies (*S. m. streckeri*) is more aggressive than the massasauga.

*Variability in Temperament*.—In summary, C. B. Perkins has this to say of his experiences with several species of rattlers at the San Diego Zoo:

As far as temperament is concerned, rattlers differ both individually and specifically. Most red diamonds (*C. r. ruber*) are very gentle. Often one is caught, brought to the Zoo, and put in a cage without sounding its rattle at all, even though the public is walking by, a few inches away, on the other side of the glass. The western diamond (*C. atrox*) puts up a big fuss in the field and most specimens continue to be nervous for a long time. The prairie rattler (*C. v. viridis*) also is excitable in the field, but usually prefers to run away instead of standing its ground as do so many western diamonds. As soon as it is in a cage, however, it usually quiets down at once. The Great Basin rattler (*C. v. lutosus*) is just about as mild-tempered as a red diamond. Some southern Pacific rattlesnakes (*C. v. helleri*) are very pugnacious but others are mild-tempered. I know nothing about eastern diamondbacks (*C. adamanteus*) in the field, but one specimen we have strikes at the least provocation. Another, here for several years, still rattles every time his cage door is opened. However, he does not assume a striking position but, instead, sticks his head out as though he were curious.

That there are differences in temperament between individuals of the same species, as remarked by Mr. Perkins, is known to all experienced field men. A few examples from among those mentioned by my correspondents may be cited:

Certain individual eastern diamondback rattlesnakes will not rattle or offer to bite, even when picked up. In fact, it is possible to reach down and slip your hand underneath them and pick them up as you would a harmless snake. I have had several that did not rattle for a month at a time, while we kept them in captivity and moved them about. Some individuals show more fight than others and some will retreat sooner than others. *Ross Allen, Silver Springs, Fla.*



I caught a large diamondback in the Okefenokee swamp that was tame from the first day I caught it. I could pick it up anywhere, place it on the ground, and then pick it up again by the middle of the body anywhere any time. I could stroke its head while it was coiled with the head raised, looking at me. This was the only tame one in all my experience. *Herbert E. Mitchell, Saint Stephen, S. C.*



Here in the Yellowstone, my only contact with rattlesnakes<sup>11</sup> has been on the north edge of the Park. Most of these snakes exhibit the same temperament, making every effort to escape. However, I found one that was extremely vicious and, when once roused, struck repeatedly and with such vigor that it was straightened out on the ground after each strike. It made no effort to escape, but kept up the fight until killed. *Harold J. Brodrick, National Park Service, Yellowstone Park, Wyo.*



Every rattlesnake seems to be different. I have come across rattlesnakes that would sneak off and try to evade me without making a sound, and again I have contacted some that would strike and rattle at the same time, that is, when approached unexpectedly. But most snakes will give you a warning in time to avoid being bitten by them, and will flee or crawl into a hole. *Gustave W. Koski, U. S. Fish and Wildlife Service, Windham, Mont.*



There seems to be a great deal of difference in rattlers. Some will try to get away, others will coil up and fight. *Lawrence Kelly, Harper, Oreg.*



Some rattlers seem to be mad all the time and always ready to fight, while others lie quiet; some will rattle as soon as they see you, and others will not rattle until handled roughly. Some will strike before they ring the bell, others will ring the bell first. What they will do is any man's guess. *J. D. Bankston, Mason, Tex.*

A. M. Jackley (1946a, p. 1), in his long experience with prairie rattlesnakes in South Dakota, found considerable individual differences, some trying only to escape, while others would defend themselves violently. He concluded that rattlers were not to be trusted, for some would violate all rules (p. 2). Others who have commented in published reports on individual idiosyncrasies are Dugès (1877, p. 15), W. (1894, p. 488), Ritter (1921, p. 29), and Storer and Wilson (1932, p. 169). I myself have noted similar temperamental variations in such forms as *ruber*, *helleri*, and *scutulatus*. I saw one southern Pacific rattler (*C. v. helleri*) that, after 3 years in captivity, still coiled and rattled when anyone approached.

Fitch (1949a, p. 518) has this to say about the variability of temperament in the northern Pacific (*C. v. oreganus*) at the San Joaquin Experimental Range:

Upon discovery, snakes, either coiled or actively prowling in exposed places, often lay motionless and did not rattle. One found prowling on a bare swale bottom even allowed a person to stamp heavily just beside its head without making any movement. When actually

<sup>11</sup> The prairie rattlesnake (*C. v. viridis*).

touched, such snakes tried vigorously to escape, sometimes without rattling or showing fight, and sometimes backing away and rattling with forebody raised threateningly in a loop ready to strike. Unquestionably temperature and other environmental factors have an important effect on behavior, but individuality is likewise important. Unusually aggressive or unusually phlegmatic behavior noted at the time of capture and handling was generally borne out by subsequent captures of the same snake under different circumstances. An occasional snake encountered was so aggressive that it would become enraged at the mere presence of a person, and would advance menacingly, rattling and striking, even though such an advance took it away from the nearest shelter. Most lack such aggressiveness, and will not even rattle until actually touched; those that do so may either make for shelter or coil.

*Factors Affecting Temperament.*—Various reasons have been suggested as the causes of these differences—sex, age, weather, environment, etc.—and some of these may be valid. Several authors consider the males more belligerent than the females, and maintain that they are particularly pugnacious during the mating season. This idea was first expressed by Dudley (1723, p. 294), and was echoed by Pennant (1787, p. 88) and Lombard (1881, p. 88). They thought that August was the mating season. Williston (1878, p. 203) believed rattlers were more aggressive in May, which he believed to be the time of mating. Stickel (1952, p. 12) thought male prairie rattlers (*C. v. viridis*) to be especially prone to attack in the mating season and females just after having given birth to young. Mrs. Florence Wood (1933, p. 85) disturbed a pair of mating prairie rattlers in Wyoming in August and found the male particularly pugnacious. A. M. Jackley had similar experiences. He wrote:

About September 1st I was going to a ranch near Mobridge, South Dakota, when I saw a prairie rattler just sliding off the grade. About 15 feet ahead, and on the other side, another was starting to cross. I stopped to catch this second snake first. The sight of the car caused him to draw back a couple of feet, but when I came opposite him, he did an unusual thing. Instead of retreating, he cautiously advanced to attack me. I stood perfectly still as he slowly advanced and when in striking distance he made an effort to strike my leg. Of course, I stepped back, about 3 steps, and still he came on and repeated the maneuver 3 times, until I had backed up to the far side of the grade. I then captured both snakes and found that the aggressive one was a male and the other a female he had probably been following. I have had a number of similar experiences with aggressive rattlers and, in all except one case, they occurred during the mating season.

John R. Hicks, of the U. S. Forest Service, Morehead, Kentucky, informed me that he thought the black timber rattlers (*C. h. horridus*), which are usually males, to be more excitable than the yellow snakes, which are generally females. Charles E. Chapin, in a communication to *Outdoor Life* (vol. 50, no. 3, p. 233, 1922), expressed the opinion that the females seldom rattle. It is true that, during the season when they are carrying young, the females roam abroad less than the males.

Although the large males are the most ready to stand their ground, particularly during the mating season, young rattlers, like the young of almost all snakes, are in some ways more belligerent than adults. Baby rattlesnakes only a few minutes after birth—indeed, as soon as they are free of the encumbering fetal cases—will coil and strike, in a pose quite similar to that of the most experienced adult. Even the end of the tail, although only equipped with the soundless pre-button, will be seen to vibrate as if in anger. The young of all snakes are subject to more hazards from enemies than the adults, and the threatening poses they

adopt may, in some cases, scare off the animals that would prey on them. Young rattlers are more likely to stand their ground in a fighting pose, and adopt the pose more readily and quickly than any other age-class.

Speaking generally, northern Pacific rattlesnakes are timid and secretive in their habits, never assuming the offensive without provocation but preferring to lie low until almost trodden on. I have only occasionally met with individuals that rattled before I was within 20 yards; very small ones are likewise less circumspect and will rattle and even strike on sight. *A. C. Mackie, Vernon, B. C.*

The environments in which rattlers are discovered will affect their reactions toward trespassers, for it is natural that they should be more prone to adopt a fighting pose if refuges are distant and difficult of access:

I've had good luck hunting rattlers on the dirt roads in the back country, starting my expeditions just before sunset. I have noticed on several occasions that if they are found on a road or in open country, they are inclined to be a bit "feisty" and more or less "on the prod." But if the vicinity affords good cover, they are more likely to go for shelter than to stand their ground. *K. R. Halstead, San Bernardino, Calif.*



It is the rattlers found traveling or in outstretched positions during the summer that seem most vicious. Those are the ones that can put up an interesting fight to elude capture; far more so than when found coiled. *Louis P. Faldborg, Chula Vista, Calif.*

Several of my correspondents make the point that a startled rattler, such as one awakened from sleep, is likely to be rather aggressive.

I have found any number of rattlesnakes coiled and asleep in the sun. Upon sneaking up to them, and touching them in the middle of the coil with a long stick, they awoke with a flash, striking in the direction in which their heads were pointing. *Morgan L. Hall, U. S. Fish and Wildlife Service, Dillon, Mont.*



I have caught rattlesnakes asleep many times. They seem very angry when awakened. *Ed Rose, U. S. Fish and Wildlife Service, Chilcoat, Calif.*



Rattlers are most dangerous when taken by surprise. *J. O. Teel, Greenville, N. C.*

Charles H. Lowe, Jr., noted a violent reaction when a little speckled rattler (*C. m. muertensis*) on El Muerto Island was awakened. Swanson (1952, p. 181) says a sleeping rattler will rattle furiously when disturbed.

Several correspondents have found rattlers more ready to defend themselves if disturbed while feeding or drinking:

During five seasons I met only two rattlers that could have been called belligerent; these were encountered when they were apparently hunting, early in the morning, and both were very definitely "on the prod" when I first saw them. *Johnson A. Neff, U. S. Fish and Wildlife Service, Albuquerque, N. Mex.*



It is believed that a rattler lying in wait for prey is more apt to strike a person or an animal passing within range, than one not so engaged. *E. L. Shults, U. S. Forest Service, Kooskia, Idaho.*



Usually, a rattlesnake attempts to avoid trouble, but if forced he will fight. If hungry, a snake will be alert and short of patience. *Ernest H. Taylor, U. S. Forest Service, Victor, Idaho.*

On one occasion I saw a rattler kill a small rabbit, and found that the snake was full of fight. I don't recall any other rattler so full of fight as this one, and I have killed many of them. I supposed it was because I disturbed him while eating. *William Hulett, Phoenix, Ariz.*

A. M. Jackley (1946a, p. 1) says that a snake that has recently fed is likely to be sluggish, whereas a hungry one may be vicious.

Rattlers are generally most vicious when going to water and sluggish after drinking. *Clarence Martz, U. S. Forest Service, Foresthill, Calif.*

Kalm (1752-53, p. 53) thought rattlers peaceable when well fed, but irritable when hungry.

The idea that the belligerency of rattlesnakes varies with the season is an old one, and may have some factual foundation, in that rattlers are certainly not active when cold. However, it is doubtful that the variation in temperament is as noticeable or uniform as commonly supposed. Brickell (1737, p. 144) thought them worst in mid-summer; Lacépède (1789, vol. 2, p. 411; Kerr, 1802, vol. 4, p. 266) thought their fury was increased by rain; Bosc (1803, p. 553) believed them most aggressive in sultry weather; Bailey (1876, p. 404; Anon., 1872b, p. 641) placed the most dangerous season just before and after hibernation; Orcutt (1891, p. 190) found the California rattlesnakes likely to attack in April, but more peaceful in June; whereas Barnes (1933, p. 398), in northern Arizona, found them particularly obstreperous in August and early September.

My own correspondents have equally divergent opinions:

It has been noted that when rattlers leave their dens in the early spring, they are inclined to be sluggish, but ill-tempered when disturbed. Later in the spring they seem to become less vicious, and will slip away if a person will permit them to do so. From the middle of July, or at the beginning of the so-called "dog days," on until cold weather and denning time, they are again more vicious. *John H. Stanley, U. S. Forest Service, Andrews, N. C.*



In Utah, in the Fillmore Mountains, rattlers appear to be "on the prod" in July and August. *C. H. McDonald, U. S. Forest Service, Stevensville, Mont.*



According to the old saying, a rattler always warns you before he strikes. Don't let anybody tell you this, because I have seen many a rattler strike, and strike again, and then be killed, and never rattle or give warning. They will generally give warning in the early part of the summer, but in the late part of summer many times they will not. *Everett W. Norris, U. S. Fish and Wildlife Service, Malta, Idaho.*



In the month of April rattlesnakes are very vicious when around their dens. When disturbed they will coil and rattle. *Jesse L. Harris, Government Hunter, Pilot Rock, Oreg.*



As spring advances and the hot dry days of summer come, the snakes on the slopes become far less numerous. If found at all, they are in a stretched-out position or crawling through the brush. Then they are of a different nature. I have known them to puff, hiss, rattle, and strike at my stick with the rapidity of a machine gun, meanwhile backing toward a bush or some other avenue of escape. *Louis P. Faldborg, Chula Vista, Calif.*

I think we may conclude from these divergent opinions that the seasonal differences that have been cited are more likely to have been caused by temperature effects or mating than the mere season itself. Fitch (1949a, p. 518), from his thorough observations of the northern Pacific rattlesnakes (*C. v. oreganus*) on the San Joaquin

Experimental Range in California, concluded that temperature and environment were the most important factors in determining a rattler's reaction toward an intruder. Jackley (1946a, p. 2) found that the prairie rattlers (*C. v. viridis*) of South Dakota were most excitable and quickest in action at temperatures of 80° to 85° F. (26.7° to 29.4° C.).

Since, in most areas inhabited by rattlers, they are largely nocturnal in summer, it is possible that their reputation for being quarrelsome at that season may result from their resentment at being disturbed, when found resting or sleeping in some cool spot in the daytime.

Finally, there is a theory that has virtually become folklore, to the effect that rattlesnakes are particularly vicious when blinded by the imminence of skin shedding; and that this occurs each year at the same time—usually stated to be August—for all snakes, which is consequently a season of particular danger.

Flint (1832, vol. 2, p. 75) stated that rattlers were most dangerous in summer when blind; however, the blindness was attributed to the absorption of venom into the snake's system rather than to skin shedding, certainly an erroneous idea. Authors who mention a belief in the danger coincident with skin shedding are Clarke (1881a, p. 27), Smith (1882, p. 672), Davis (1889, p. 182), Reese (1910, p. 367), Coleman (1930, p. 108), Brendle and Unger (1935, p. 200), King (1941, p. 59), and Ramsey (1945, p. 37). The increased irritability is usually attributed to partial blindness, but some authors mention an increased virulence presumed to result from venom conservation, as being the source of the added danger.

My own correspondents have made the following comments on the effect of skin shedding on rattlesnake dispositions:

Rattlers are most dangerous when they are shedding their skins, as they are blind and will strike at anything that comes near. This happens in August. *Calvin A. Bowman, U. S. Forest Service, Deer Lodge, Mont.*



I had a very interesting day yesterday running my getter [trap] lines, picking up four rattlesnakes. I was under the impression that they were blind during the month of August. So, to satisfy my curiosity, I took a shovel and moved it above their heads in every direction and they never missed striking it once. So, our rattlesnakes are not blind during the month of August. *Joe R. Bachlet, Wheatland, Wyo.*



In August, a few years ago, Robert Hamby, of Kimberly, Idaho, came upon a rattler evidently in the process of shedding its skin. He observed the snake was blind at that time and struck in all directions, or in every-which-way, as he expressed it. *Merlin R. Stock, U. S. Forest Service, Twin Falls, Idaho.*

That the belief in the August shedding-season danger has become so widespread as to be virtually folklore is shown by its frequent mention in the questions-and-answers columns of the nature and sporting magazines. It was made the crucial element in the plot of one of Thomas Beer's short stories (1921, p. 16).

A diametrically divergent theory of the effect of shedding, one that would make a rattler less dangerous during this period, is the following:

A friend of mine contended that during the heat of the summer, rattlesnakes would not strike. His theory was that they were moulting and their mouths were tender, or the tissues immediately adjoining were. *Meredith Leitch, Staunton, Va.*

As I have shown (p. 359) in discussing the shedding operation, snakes usually shed more frequently than once a year—this is particularly true of the adolescent period of rapid growth—and the shedding season is therefore not restricted to a particular time of year. Furthermore, the period of partial blindness is a relatively short one; it occurs a few days before, rather than immediately before, the skin is shed. For their own protection, snakes probably seek seclusion during this period of defective eyesight and thus should not be especially dangerous. Captive snakes show no particular irritability during the “blue-eyed” stage when the spectacles over the eyes are dulled by the accumulation of liquid beneath. Doubtless a partially blind snake would be more likely to strike, owing to a feeling of helplessness, if closely approached in its seclusion during the short period of dull vision. That the accumulation of venom during this brief period would notably increase the snake’s virulence—not to be confused with its irritability—is to be doubted, since the period of inaction owing to skin changing is short when compared to the normal feeding intervals.

#### PROTECTIVE COLORATION AND CONCEALMENT

Having discussed the temperament of rattlesnakes and some of the causes of its variability, I shall now describe the successive actions that most individuals follow when confronted by a dangerous enemy such as man.

The first reaction is almost always to lie quiet in the apparent hope of escaping discovery—to “lie doggo,” as the British slang phrase has it. For most rattlesnakes are protectively colored, that is, their colors and patterns are such as to blend into their surroundings, so that they are difficult to see, unless the eye be caught by some movement. This dependence on procrypsis is no mere policy of doing nothing, nor does it result from the snake’s not having discovered its enemy. On the contrary, it is deliberate—the result of instinct, intelligence, or whatever term may be applied to the snake’s attempt to attain a particular goal. That the rattler is alert to the trespasser is sometimes shown by a flicking out of the questioning tongue, or a premonitory click as the tail is adjusted to sound the rattle should this be found necessary. Several of my correspondents comment on the evident design behind this rattler method of avoiding trouble:

When you see a snake crawling before it sees you, or one lying stretched out and at rest, and you proceed as if to pass close by, it will most likely freeze, which presumably is an instinctive way of avoiding detection. If you stand perfectly quiet by its side, in a few seconds the snake will slowly thrust out its tongue as an indication of growing nervousness. *A. M. Jackley, Pierre, S. Dak.*



It is not uncommon to find rattlers stretched out, playing possum, so to speak, not making a move until prodded or otherwise disturbed. Of course, as soon as they see that their whereabouts are noticed they will coil and rattle, and prepare to defend themselves. On almost every occasion, however, they will escape if it is possible to do so. *L. J. Cooper, U. S. Forest Service, Galice, Oreg.*



I have found it quite amusing to watch rattlesnakes lying quietly, hoping to escape detection. Upon finding they are discovered, their first impulse is to beat a hasty retreat, but, if escape is impossible, they don’t hesitate to stand their ground. *A. W. Mollison, U. S. Indian Service, McNary, Ariz.*

I found one rattler by noting its track across the road. Careful inspection of the track pointed to the direction taken and I saw the rattler about 30 feet off to the side of the road, stretched out and motionless. I took time to fish the collecting tools from the trunk on the car and then walked over to within a couple of feet. The rattler remained "frozen" until I touched its neck, when it suddenly became the active creature that *atrox* usually is under such conditions. *Charles M. Bogert, American Museum of Natural History, New York, N. Y.*



I have observed rattlers that would not move, as they thought—if you can call it that—that they were hidden, and only coiled and rattled when hemmed in. *Joseph T. McCullough, U. S. Forest Service, Brooklyn, Miss.*

On two occasions I have passed very close to snakes—both speckled rattlers, *C. m. pyrrhus*—without seeing them, and then have had my attention drawn to them by some movement that caused a slight noise. How many I have passed without their making this fatal mistake I shall never know.

This habit of depending on the concealment of protective coloration has long been known; it is mentioned by Wood (1634, p. 48), who thought the rattler asleep; the habit was also described by such early observers and travelers as Kalm (1752–53, p. 316; 1937 ed., p. 614), and Bossu (1771, p. 363). That the instinctive ruse is often successful there can be no question. On several occasions I have tried the experiment of informing a companion not experienced in hunting rattlers, that one was in plain sight in a patch of rocks or brush within a circle, which I roughly indicated, and then have asked him to point it out, without, of course, approaching the spot. It was each time surprising to see how long it took him to locate the snake. This affords a convincing evidence of the effectiveness of protective coloration.

People not accustomed to seeing rattlers can't see a snake even when their attention is directed to it. *A. M. Jackley, Pierre, S. Dak.*



One soon cultivates a snake-eye which enables one to spot a snake, however protectively colored or concealed. Those unfamiliar with rattlesnakes can hardly see them when their whereabouts are pointed out. *A. C. Mackie, Vernon, B. C.*

Hogner (1938, p. 127) tells of a snake hunt in which he secured 6 rattlers within half a mile, yet the people who lived at this place had never seen one.

This rattler habit of lying motionless is one of the most frequent causes of accidents. For the inexperienced passer-by, failing to see the snake that hopes to escape detection, may put his foot within the danger zone, or actually step on it, without being aware of its presence. Then, frightened or hurt, the rattler may quickly change from inaction to action and a bite results.

Sometimes when rattlers are hidden, they will remain stationary and then strike; this is the reason why many livestock are bitten on the head. *Drayton Wasson, U. S. Forest Service, Española, N. Mex.*



I have seen only one rattlesnake which did not make an effort to escape when I encountered it; I think the reason for this was that another person had just walked past the reptile without seeing it, but had roused it, and I came along in time to receive its anger. *Earl Jackson, National Park Service, Las Vegas, Nev.*

This last is an example of a fairly frequent occurrence, wherein the first person in a party along a trail alarms an unseen rattler that may strike one of those who follow behind the leader.

Bailey (1905, p. 51), commenting on his experiences with the mottled rock rattlesnake (*C. l. lepidus*), says:

On the dark-brown lava soil they are very inconspicuous and they had a way of suddenly springing up between our feet that made us highly nervous.

I have discussed elsewhere (p. 221) the degree to which rattlesnake patterns do aid in the success of procrypsis as the initial step in their protective behavior. In general, their color variations can be ascribed to the nature of the rocks, soils, and vegetation wherein they live, although there are several exceptions to the rule. W. T. Neill advised me that the perfection of the procryptic coloration of the eastern diamondback (*C. adamanteus*) is such that it is holding its own in northern Florida, whereas its mammalian and ophidian competitors for prey are being decimated by the increased human population, with its attendant agricultural and commercial developments.

The rattlesnake's successful concealing coloration is probably equally useful as a protection against enemies and in enabling it to ambush its prey, for the two purposes are not in conflict. Some animals with dangerous or injurious attributes—the skunks, for example—advertise their presence by a conspicuous warning coloration that any predator learns to avoid. The rattlesnake does not need this kind of advertisement, since, for the purpose of warning, it can and does fall back on the strident rattle and a fighting pose whose intention no creature can misjudge.

To some early writers, the idea that rattlers depend upon procrypsis for protection would have seemed impossible for two reasons: There was, first, the widespread idea—it has now become folklore—that rattlers give forth so strong an odor (and this independent of the use of the postanal scent glands) that their presence is easily detected, even when they are resting undisturbed. I have discussed this more fully in chapter 18 (p. 1269). The second is that the slightest movement of the snake causes the rattle to sound involuntarily, also an ancient misunderstanding upon the part of those who had not seen a live rattler in action, and thus had no opportunity to observe the silence of the rattle unless it be deliberately vibrated. Moore (1744, p. 59) mentions these as reasons why rattlers are always easily detected by anyone long before getting dangerously near one.

#### FLIGHT

In the instinctive ruse of lying motionless and depending on concealing coloration proves successful, and the intruder leaves without discovering the rattler, the latter may continue to remain without movement; or it may, after a short interval, crawl toward a safer refuge. But if the enemy shows, by coming nearer the snake or by adopting a belligerent attitude, that the ruse has failed, then the rattler may attempt retreat, or it may throw itself into a striking coil and threaten the intruder. In fact, it frequently does both at once; for the striking coil permits a snake, while facing the interloper and ready to lunge if he comes within range, to retire at a good rate toward any available sanctuary.

There is a considerable variability in the conditions under which individual rattlesnakes will abandon procrystis in favor of flight. Some will endeavor to escape while the supposed enemy is still some distance away, whereas others will continue to lie quietly until all hope of avoiding discovery is surely gone. Jackley (1945a, p. 1) believed that usually one may walk close by a rattler and it will remain quiet, but if one walks toward the snake it is more likely to rouse itself, either for flight or battle. He tried walking past a rattler at distances of 10, 5, and even 2 feet without result, but the snake reared up when he walked directly toward it. He agreed that people pass by many more snakes, without seeing them, than they ever discover.

Rattlesnakes, when lying about in the open, generally remain near places of refuge; of this there can be no question, and their prompt and direct manner of availing themselves of concealment in the refuge leaves little doubt that this is an intentional expedient or an instinctive habit. It is a common observation when the snakes are scattered about outside their hibernating dens, taking advantage of the last sun of the autumn or the first of spring. Many collectors have reported how necessary it is to get between the rattlers and their holes, toward which they streak as soon as they become aware of an intruder. The same is true on a less impressive scale when single rattlers are met on their summer ranges. I have on several occasions found southwestern speckled rattlers lying in front of horizontal rock crevices, in which they took refuge so quickly and directly that the use for this purpose must have been premeditated. Charles H. Lowe, Jr., noted that the little speckled rattlers found on El Muerto Island were always near safe retreats in rocky crevices or holes. He thought this might be in order that they could quickly take refuge from the heat. Another instance of a snake maintaining a refuge available against either enemies or heat is the following:

On one occasion in the company of Dr. C. T. Vorhies and Robert Flock, I had an opportunity to witness what might be termed either intelligence or some type of rattler "instinct." During the summer of 1940 when we were collecting bats, a black-tailed rattler (*C. m. molossus*) was found asleep near the entrance of a mine tunnel on the southwestern slope of Picacho Peak, near Picacho, Arizona. As it was a good adult specimen of a not too-common species, we decided against killing and in favor of catching it in a butterfly net and releasing it in a clump of rocks some 30 feet from the tunnel entrance. About half an hour later we were surprised to see the rattler (the same individual, judging from size and coloring), slowly working its way through the rocks toward the entrance to the mine. At times its head was raised as if looking over the situation. When we annoyed it with a stick in an effort to get it to change its direction, it would somewhat withdraw among the rocks but would still continue to move in the general direction of the mine opening. It was only by constant prodding that we were able to keep the snake away from the mine while we were collecting bats. Although it was a cloudy day, it is possible that the snake, through some form of intelligence or instinct, sensed the fact that if a change occurred in the weather, it had better be in close proximity to the relatively cool refuge afforded by the tunnel. Lee W. Arnold, U. S. Fish and Wildlife Service, Denver, Colo.

That most rattlers do attempt to escape, instead of stopping to give battle, is generally agreed by those of wide experience in the field. Early expressions of this conclusion will be found in Lahontan (1703, p. 357), Jones (1724, p. 51), Kalm (1752-53, pp. 53, 317), and Hewatt (1779, p. 86). Some of the observations of my own correspondents upon the rattlesnakes found in their regions are as follows:

My experiences with the timber rattlesnakes here in Virginia lead me to believe that they would prefer to go unnoticed rather than face an adversary. They do not rattle until disturbed or approached too closely and then endeavor to get under cover. *Charles O. Handley, U. S. Fish and Wildlife Service, Blacksburg, Va.*



In all my encounters with rattlers, they made every effort to get away. If bothered sufficiently, they would coil and strike, and then try to move on again. *Harold J. Brodrick, National Park Service, Yellowstone Park, Wyo.*



I killed 32 rattlesnakes in the Lake Chelan vicinity, Washington, one summer while working on a timber survey. I never found one that wouldn't run away. (*Author's name omitted by request.*)



I have never had any case where a rattlesnake did not try to get away if given a chance. Of course, if he was poked with a stick or molested in any other such manner, he would show fight. *J. T. Kenney, U. S. Forest Service, Dardanelle, Calif.*



Regarding the fighting qualities of rattlers, I have never known them to take the offensive. Their fighting and striking are merely for their own defense. It is only after they are molested that they show activity, for their first inclination is to escape. *Louis P. Faldborg, Chula Vista, Calif.*

An escaping rattler will usually try to crawl away as rapidly as possible, taking advantage of any cover it may reach. If, however, it is threatened or closely pressed, it will adopt a defensive coil with the head and fore part of the body raised above the ground and poised in an S-shaped loop, so that it can lunge forward and strike if the enemy approaches within reach. But, while the snake thus faces the intruder, the posterior part of the body writhes in such a way that the snake crawls backward toward the nearest bush, rock, or other refuge; in military parlance it executes a rear-guard action. One of my correspondents describes the maneuver thus:

This prairie rattler, when I disturbed him, tried to get away, but, on following him, he coiled in the usual manner, his head above his coils ready to strike. The movements of this snake interested me. His coils seemed to tighten up and then relax, and I noticed that he was gradually moving away from me, though still ready to strike, and was most certainly putting distance between us. *D. A. Fleming, Swift Current, Sask.*

When a rattler is thus retreating in its fighting pose, it will sometimes move toward the enemy, if the nearest place of concealment lies in that direction. In one case a sidewinder on the road came directly toward me, but there is little doubt that it was merely seeking the protection of the car near which I stood, and which must have seemed a kind of refuge to the snake. My correspondents mention similar instances:

While hiking up a narrow canyon in the Ruby Mountains of Nevada, I heard a rattlesnake and at the same moment saw, 12 feet away, a snake about 30 inches long coming rapidly down a steep, barren slope toward me. Had I retreated at that moment, I would have been certain that the snake was attacking. Instead, I stood my ground, and it took refuge under a bush 5 feet from where I stood. It was then evident that I had surprised the snake in the open, and in order to gain cover, it had to come toward me. Under the bush it remained silent and motionless. *A. E. Borell, Regional Biology Division, Albuquerque, N. Mex.*

I recall on one occasion that my companions swore a northern Pacific rattlesnake gave chase after me, who failed to suspect its presence, even crossing over a large fallen log. Actually, it seemed to be seeking a dark recess under the log for escape. *John Dern, San Francisco, Calif.*

Langford and Gibson (1952, p. 116) mention an instance in which a rattler went toward a man who stood between the snake and a hole it sought as a refuge.

If there is danger that a rattler one wishes to capture or kill may escape, the simplest maneuver is to annoy it sufficiently so that it will stand its ground to defend itself, while a weapon is being sought.

If I run across a rattlesnake and haven't anything at hand to kill it with, I pester it enough to get it really mad and then it will stay put for some little time while I look for a heavy stick or bunch of rocks. *J. Fred Toman, Bowers, Mont.*

Allison (1946, p. 47) even claims that if one throws a hat or coat at an eastern diamondback (*C. adamanteus*), it will coil and watch the clothing, while a suitable stick for catching or killing it is being sought. Carrying this ruse further, McCulloch (1918, p. 5) thought that one might throw down his hat, thus diverting the snake long enough to permit a person to escape (as if such an expedient could be necessary); and Voelgyi (1926, p. 140), a Hungarian traveling in Texas, even reported that if a woman found herself without a gun (obviously a rare occurrence in that state) when confronted by a rattler, she would hang a piece of cloth on a bush and run, secure in the knowledge that the snake would watch the cloth for hours, thus permitting her to escape. Higgins (1873, p. 86) stated that if you should throw a hat down in a snake's path, it would immediately coil around it and defy you to take it away. But enough of fantasy.

Sometimes a refuge-seeking rattler adopts a ruse that may well be dangerous to an inexperienced pursuer, as is evident from the following observations:

As soon as a rattler enters a hole for a few inches, the head will turn again toward the entrance, while the rest of the body is being pulled into the hole behind the head. Then if you try to catch the disappearing snake you will surely get bitten. *Gustave W. Koski, U. S. Fish and Wildlife Service, Windham, Mont.*



One rattler crawled in a hole, leaving his tail protruding several inches. I nearly fell for this trick, but noticed his head just inside the hole, apparently ready to strike when I reached for his tail. *Wm. F. Poley, U. S. Forest Service, Monte Vista, Colo.*

It has been stated that an escaping rattler on a hillside will almost always head downhill, thus making better speed. This is certainly not invariable; it is probable that the nearest bush or rock crevice that might serve as a refuge more often guides the direction of escape.

#### DEFENSIVE ATTACKS

I have pointed out that rattlers differ in their temperaments, both individually and specifically, and that their reactions to an external threat are not only affected by these differences, but also by the circumstances and surroundings in which they are discovered. Though I have suggested that rattlers usually go through two phases of passive defense—procrystis and flight—before adopting a fighting pose, this is by no means universal, and no one should be so foolish as to depend on

their adherence to this sequence. My correspondents cite numerous instances of various deviations from this program—of snakes that adopted the final fighting pose without preliminaries, and others that even pursued an active offensive. I have elsewhere (p. 713) mentioned a few such cases that occurred during the mating season and were presumably evidences of the possessive actions of the males. Here are some further reports, not thought to have any sexual basis, of rattlesnakes attacking men:

Upon one occasion I was traveling on foot early in the season and encountered a small rattler, 21 inches long, which struck at me when I was more than 3 feet away. As I backed up and started to pull my gun, the snake came at me and struck again. I backed up again, and this was repeated until I had backed up 18 feet, when I shot the snake. *Irvin C. Robertson, U. S. Forest Service, Salmon, Idaho.*



Usually rattlers try to crawl away, but occasionally they will coil and hold their ground. We have even noted a few cases in which they would start toward a person, striking as they came, making it necessary to retreat or kill the snake. *Harvey E. Zink, U. S. Forest Service, Sawyers Bar, Calif.*



In Sheep Canyon, off of Lytle Creek, I had a rattlesnake deliberately pursue me. I changed the direction of my retreat several times to check on this, and each time the snake kept right after me. *C. S. Wynne, U. S. Forest Service, Idyllwild, Calif.*

Dr. Cyrus N. Ray, of Abilene, Texas, has written me of two instances in which he was attacked by western diamond rattlers (*C. atrox*). In one case he struck at the same time that the snake struck at him. Both missed, whereupon the snake pursued him in a series of advancing lunges, until he was able to turn and, running a short way, obtain a rock, with which he killed it. In the second experience substantially the same thing happened. I wrote Dr. Ray asking whether there was any possibility that the snakes were merely seeking a hiding place, when they appeared to attack him. He replied:

In reference to your idea that the snakes observed were trying to get away and only incidentally came in my direction, I wish to state that they both took the hard way to get at me, and if I had been slow in my movements I feel that my opportunity to write this would not have occurred. The Blowout Mountain snake pursued me up a rather steep embankment when the easy way was out on the level below, where flat land and brush cover lay. The snake found near Ft. Chadbourne, in Coke County, was lying on level ground beside a road. The land was all level, and beyond the fence bordering the road were shrubbery, cactus, grass, and mesquite trees, which would have furnished some cover for the snake. But as I approached from the smooth roadway to hit him, he struck first, and advanced on me out into the clear and onto the beaten roadway so fast and furiously that I feared to risk trying to hit him with the stick, and ran to get rocks to stun him with, when I then closed in and killed him.

Dr. Ray also told me of another instance in which a friend of his was chased around a clump of cedar trees by a western diamond before he could get far enough away from the snake to seize something with which to kill it. Of course, with regard to these instances of attack no one should presume that any rattler could move fast enough to overtake a man who really wished to get out of its way. The only danger would be that, while backing up in order to watch the snake's movements, one might trip over something and fall in its path.

One writer gives an idea of the relative infrequency of such attacks:

A friend of mine says that, of the several hundred rattlers he has seen, only three came forward toward him as if to attack rather than seek shelter, or hide under a bush or in the rocks. *E. J. Parker, U. S. Forest Service, Ukiah, Oreg.*

In several instances of apparent attacks, horses were involved, leading to a possible assumption that rattlers may find the odor of a horse offensive, although it is much more probable that a horse alarms the rattler by its heavy tread:

One day while hunting coyotes in midsummer, I was riding horseback around the side of a steep hill when I heard a snake rattle. Looking up, I saw a rattlesnake striking and throwing itself down the hill toward me. It was about 10 feet up hill from me when it started. It would throw itself, and as soon as it hit the ground it struck again. It kept this up until it passed under the belly of the horse I was on. It stopped about 5 feet below me under a bushy tree. *Morgan L. Hall, U. S. Fish and Wildlife Service, Dillon, Mont.*



I have never taken much stock in the old story of a rattlesnake attacking a person; but some years back, near Datil, New Mexico, in September, I had snakes charge toward me on two occasions; but, in the excitement of getting them killed, I failed to try to figure out just what was causing their actions or reactions. I was on horseback, so it is possible they just charged the noise. *W. H. Koogler, U. S. Forest Service, Prescott, Ariz.*



Generally, rattlesnakes will attempt to retreat when you come in their path; although one year, on two occasions on steep mountain trails, I have had them coil and actually crowd my horse from the trail. *Lee Kay, Utah Fish and Game Commission, Salt Lake City, Utah.*

Obviously some rattlesnake attacks result from an initial hostile motion of the person making the report, but at other times it is impossible to determine what first aroused the snake. Stanley G. Jewett, of Portland, Oregon, had a northern Pacific rattler strike at him as he went by on a rocky slope to retrieve a duck he had shot on a nearby pond. Fitch (1941a, p. 518) reported that, although most northern Pacific rattlers on the San Joaquin Experimental Range lacked aggressiveness, occasionally one would come out striking wildly, even if this led the snake away from its shelter. Hall (1929, p. 80) tells of a Great Basin rattler that took the offensive and approached several men with aggressive intent, covering a distance of about 12 feet. The men were experienced naturalists, familiar with rattlesnakes in the field; this is not the report of a frightened observer, as is often the case in accounts of aggressive rattlers.

I have already pointed out that it is risky for persons to pass in single file along a path, since the head of a party may disturb a rattler sufficiently to cause it to strike one of those who follow. Sometimes a snake is disturbed by passing animals just as a man comes along:

I have seen only one rattler that was "on the fight." A band of sheep had just passed over or around it. It was coiled at the foot of a large ponderosa pine tree and had about one-third of its body off the ground waving from side to side and rattling vigorously all the time. *Earl C. Sanford, U. S. Forest Service, Vernal, Utah.*

Of course, it is to be expected that an injured snake will attack. For example:

The only act of aggression I have witnessed from a rattler was an instance where a diamond-back had been shot by a rancher. When the man approached, the snake attacked him unsuccessfully, but in this case the snake was obviously pain-crazed and had been biting itself. *Philip F. Allan, Soil Conservation Service, Fort Worth, Tex.*

I stepped on a rattler one warm day, and he struck and bit me on the side of the leg. He then took right after me until the dog ran in between us, and the snake then took after the dog, until I shot the rattler. *Elmer C. Bernasconi, U. S. Fish and Wildlife Service, Altaville, Calif.*

It may be said, in passing, that these rare instances of aggression are not restricted to rattlers or even to venomous snakes. For example, Wade (1945, p. 172) gives a well-authenticated account of an attack by a large pilot black snake (*Elaphe o. obsoleta*) that he had just released. Similar stories of attacks by harmless black racers (*Coluber c. constrictor*) are common (e.g., Noble, 1937, p. 683; Finneran, 1948, p. 123).

It would be regrettable if, owing to their sensational nature, these reports of occasional rattler aggressiveness should lead some of my readers to impute a great deal more vindictiveness to rattlesnakes than they deserve. I could cite plenty of evidence to the contrary, although naturally much less exciting. Some reports that represent more usual attitudes follow:

I have never seen a rattler strike if given any chance to get away, and have always found it necessary to run them down, kick sand at them or in some way irritate them before they would show any fight. *Dwight A. Hester, U. S. Forest Service, Grand Mesa, Colo.*



Usually when rattlesnakes are disturbed they are not ready at once to strike, but will crawl away, raising their heads some distance above the ground and rattling rather casually. When notice is taken of them, in most cases they will try to escape, but failing this they coil, ready to strike. *R. C. Anderson, U. S. Forest Service, Ogden, Utah.*



As a rule, the northern Pacific rattlesnakes in this area are prone to lie still or try to escape if a person approaches. They usually do not rattle unless a person steps very close to them and they are already coiled. I have stepped right alongside of several rattlesnakes that were stretched out and would never have known they were there, had I not seen them. Upon being prodded with a stick they immediately coiled and rattled, and showed they were ready to fight. *L. J. Cooper, U. S. Forest Service, Merlin, Oreg.*



In all my experience, from the deserts of southern California to the high mountain regions, I have never known a rattlesnake to attack, or even to stand and fight a human being when there was the slightest opportunity for the snake to make its escape. *A. Lewis, U. S. Forest Service, Groveland, Calif.*



Virtually all the rattlesnakes I have ever found tried to get away from me and very seldom showed any fight until they were attacked. *F. A. Land, U. S. Forest Service, Sierraville, Calif.*

Several of my correspondents report instances of failure to strike even when the opportunity offered:

A girl of my acquaintance was sitting on a log with her feet resting on the ground. After she had been sitting there for some time, she moved both feet up on the log, and while in that position she glanced down the other side of the log and there was the coil of a black rattler. Her feet had been within easy striking distance, but no effort was made to strike, nor did the snake rattle. *C. V. Dong, State Fish Warden, East Waterford, Pa.*



I once stepped on a coiled rattlesnake I did not see lying on the trail. He neither rattled nor struck at me, nor did he rattle when I killed him. He was lively enough, and about 3 feet long. *B. A. Eger, U. S. Forest Service, Buena Vista, Va.*

Once while cradling grain in my uncle's field, he called to me to come back, and pointed to a large rattler all coiled up and in position to strike. I had stepped within 2 or 3 inches of the snake. In picking up the grain my uncle had run the back of his hand on it; he felt something cold which caused him to look down and see it. The snake was perfectly quiet and showed no disposition to bite. *A. A. McCoy, Hines, Oreg.*



On one occasion I sat down beside a big rattler and did not know of its presence until I heard it moving away through the grass. It never rattled, but seemed intent on leaving my company. I have never found one aggressive; they are content to be left alone. *Nelson K. Carpenter, San Diego, Calif.*

That rattlesnakes are generally peaceably inclined, unless deliberately provoked, has been commented upon by many of the early writers, prone as some of them were to exaggerate the dangers from the wild creatures of the New World. This pacific attitude has been mentioned by Hernández (1615, fol. 192r; 1628, 1651, p. 329), Wood (1634, p. 47), Nieremberg (1635, p. 268), Jonstonus (1653, p. 27), Budd (1685, p. 35), Clayton (1693, p. 39), Hennepin (1698, p. 221), Lawson (1709, p. 128), Beverly (1705, p. 64; 1722, pp. 64, 260), Catesby (1731-43, vol. 2, p. 41), Purry *et al.* (1732, p. 1017), Brickell (1737, p. 143), Kalm (1752-53, p. 318; 1758, p. 292), Charlevoix (1761, vol. 1, p. 244), Timberlake (1765, p. 45), Crèvecoeur (1782, p. 238), La Rochefoucault-Liancourt (1799, p. 595), Weld (1800, p. 150), Dwight (1823, p. 29), and Bailey (1878, p. 404). In addition to pointing out the inoffensive character of these snakes, the writers dwell on the warning usually given by the rattle, and the fact that generally they must be deliberately disturbed to become dangerous. Similar data, with some more recent experiences, are given by Grinnell and Grinnell (1907, p. 50), Reese (1910, p. 367), Grinnell, Dixon, and Linsdale (1930, p. 153), Sprunt (1933, p. 24), King (1939, p. 577), Gibson (1940, p. 24), and Maloney (1945, p. 30).

Even after a rattler has taken an offensive attitude it is quite possible to cow it so that it will no longer attempt to strike, but will only hide its head in its coils.

A rattler can be frightened to the point where it won't strike. I have seen this done. *Ellen Johnston, U. S. Fish and Wildlife Service, Shelby, Mont.*

Wilbur Doudna reports having deliberately teased and abused a Panamint rattler (*C. m. stephensi*) in an endeavor to rouse it to anger, but without success.

The idea that a rattler can be cowed by abuse should not be depended on for protection short of killing the snake. There is nothing to warrant the statement by Wood (1855, p. 332) that, when a rattler is ready to strike, one has only to clap his hands or rap the ground with a stick, whereupon the creature will be so startled—like a man awakening from sleep—that it will “fall out of its coil.” Besides the fact that the snake is unable to hear a sound made by clapping hands, such a sudden motion would only stir it to greater belligerency.

#### WARNING MECHANISMS

*The Rattle.*—One of the principal elements of the rattlesnake's standard warning behavior is the use of the rattle, for the primary function of the rattle is to warn away or frighten animals that might be injurious to the snake. This presently accepted theory of the purpose of the rattle, which I have discussed in chapter 5

(p. 257), requires mention at this point only to the extent of indicating the variability in the use of the rattle by a snake on the defensive.

In the early days, those who wrote on natural history were so impressed with the unique character of the rattle that they stressed its use as a God-given benefit to mankind, believing that no rattler ever struck without first giving fair warning by rattling. Later observations failed to confirm this, and from time to time controversies on this point have raged in the questions-and-answers columns of the sporting magazines in which both sides have bolstered their theories with field observations. Actually, the evidence points to the general conclusion that rattlers usually warn before striking, and that a clarification of definitions would compose some of the apparent differences between those who have maintained opposing views. For the question naturally arises as to what one means by the term "strike." If this is thought to be synonymous with "bite," then certainly rattlers do not invariably warn an enemy (they never warn prey); for if one steps on a rattler it will quite likely bite without even striking; and if a rattler is suddenly and violently alarmed it may strike instantly, and may or may not rattle simultaneously. The procedure is largely a matter of timing; if a rattler is annoyed by an approaching enemy, and it is given time to shift from procrypsis and flight to active defense, then in nearly every instance it will throw itself into its menacing, S-shaped coil, and at the same time it will sound the rattle. But if an attack comes suddenly, the rattler may retaliate with an instant strike, and there will be no interval of rattling. Certainly no one should expect a rattler to advertise its presence by rattling when there is a chance that it may escape detection by depending on concealing coloration and quiescence, since this would obviously defeat its purpose. Yet many take this as a failure to deliver the much-heralded warning.

Among the authors who supposed that rattlers never failed to warn before striking were Beverly (1705, p. 64; 1722, pp. 64, 261), Walduck (1714, in Master-son, 1938, p. 215), Vigne (1832, p. 90), Lanman (1863, p. 229), and Wood (1863, vol. 3, p. 102). Only one of my correspondents takes this position, and he merely states that in his experience he never saw one strike without first sounding the rattle. Pistorius (1763, p. 80) enunciated the strange theory that rattlesnakes always rattle three times before striking. This has now become a part of the folklore of Maryland (Bergen, 1899, p. 87; Whitney and Bullock, 1925, p. 60) and of the Pennsylvania Germans (Brendle and Unger, 1935, p. 200).

Of the authors taking the other side of this argument, none takes the position that rattlers never warn; most of them are merely concerned with the widespread belief that they always warn, a theory they wish to correct in the interest of safety. Kalm, as early as 1752-53 (p. 316), expressed the opinion that they sometimes failed to rattle before biting. Le Conte (1853, p. 419) believed that rattlers seldom warn before striking. Wright (1900, p. 256), V., C.A. (1913, p. 498), Gillam (1916, p. 130), Magee (1913, p. 87), Benton (1945, p. 80), Small (1946, p. 88), and Breland (1948, p. 199) cite instances of failure to warn, but some of these fail to differentiate between bites and strikes.

Swanson (1952, p. 181) believes that a suddenly alarmed rattler, such as one that is found asleep, is more likely to rattle than one already on the alert. Duncan

(1915, p. 171) thinks a rattler will usually sound the rattle if found in the open, but may not if partly concealed.

Artran (1940), who hunted rattlers assiduously in California and Arizona, states that only 2 or 3 per cent of the snakes he caught rattled before he saw them. This is hardly to be construed as an arraignment of rattlesnakes for failure to warn; rather, it shows the extent of their dependence on procrypsis. The rattle, in fact, is the poorest kind of a defense against man, for in his case it invites, rather than discourages, attack. We may be sure that had there been missile-throwing and weapon-carrying creatures on earth during the aeons when the rattle was being developed, the ancestors of the rattlesnakes would never have survived to bequeath this queer appendage to their descendants of today.

The following are some of the varying opinions of my own correspondents upon the readiness with which the snakes sound their rattles. It is to be noted how frequent is the assumption that a really fair and honest rattler ought to sound off and make its presence known whenever a human being comes within hailing distance:

Without having statistics to prove it, I think that rattlesnakes will fail to warn by rattling about one-third of the time. This does not seem to be a seasonal characteristic. Most snakes I have come in contact with rattled when closely approached, say at about 10 feet or less. I remember one last year that gave its warning when over 30 feet away. *Meredith Leitch, Staunton, Va.*



I am convinced that rattlers do not always rattle before striking, as I was struck on the heel by one in Tennessee. The snake was lying beside an old railroad grade and did not rattle before striking. *T. S. Seely, U. S. Forest Service, Talladega, Ala.*



Rattlesnakes do not always act the gentleman, as so often is said of them, for just today, one struck at me and rattled at the same time. *Phil. Kennedy, U. S. Forest Service, Douglas, Ariz.*



I have almost stepped on rattlesnakes possibly a dozen times, but the only time there was a warning rattle was once in a canyon near the Coral Reef Ranch south of Indio, California. My wife was approaching a paloverde bush to observe a verdin's nest, when a rattler produced a whirr that was a compensation for all the other cases of omission. *Josiah Keely, Huntington, N. Y.*



As for a rattler always warning you, I have not had one in 20 do any rattling except when fought with a stick or rocks, and often not then. While I will always go out of my way to kill them, I highly respect them because quite a number have had every chance to sink their fangs into me and didn't. One tried once, but only because I was standing on his tail. Don't tell me a man can't jump 6 feet high without bending his knees first. *R. J. Yates, Game Warden, San Rafael, Calif.*

So universal is the folklore belief that a rattlesnake always rattles before striking, that a note of warning may not be amiss:

There is one thing I would like to see more publicity given to. That is the fact that a rattlesnake does not always rattle. In fact, I have not heard one rattle except when he was very much provoked. The one that bit me did not rattle at all; and just this last week while dove hunting, my companion walked within 3 feet of one that was coiled, and I, following him, almost stepped on it. The movement of the snake's head attracted my attention, and even then it did not rattle, merely watched me as I was only a few feet from it. *G. M. Robinson, in Outdoor Life, vol. 68, no. 5, p. 108, May, 1929, writing from California.*

Some people, not knowing of the rattlesnake's usual expedients of procrypsis and retreat, express surprise and shocked loathing for the faithless rattler that fails to sound off at the moment when it is first discovered by a human intruder, regardless of the distance that separates them. I have already pointed out that rattling is usually a later element of the defensive sequence.

*The Hiss.*—A second element of the rattler warning posture is the hiss. It is surprising how many writers have stated that rattlers cannot hiss, among them Mather (1873, p. 278), Hopley (1882, p. 313; 1887, p. 512), Ingersoll (1884a, p. 402), O'Reilly (1891, p. 87), Lydekker (1896, p. 242), Fountain (1901, p. 80), Hudson (1919, p. 205), Thompson (1924, p. 71), and Sass (1935, p. 258). The assumption has evidently been that they do not need a warning hiss, as do other snakes, its place being taken by the rattle. As a matter of fact, rattlers can and do hiss quite loudly, although it is true that the sound is largely overshadowed by the more strident rattle. But it is only necessary to still the rattle by tying a bit of cloth around it, and the unquestioned hiss will be heard from any rattler in its striking pose. S., E. gave an accurate description of a rattler's hiss as early as 1883 (p. 7). The hiss compares favorably in volume with that made by most other snakes, although not so loud as some, such as the bull or gopher snakes (*Pituophis*), which have a special formation of the epiglottis to increase the sound.<sup>12</sup>

A rattler may hiss on either inspiration or expiration, or both. There is little difference in the volume of sound produced, although it seems slightly more intense upon exhalation. Sometimes the whole body swells or deflates, sometimes only the anterior half, while the posterior flattens, as is usual in the threatening posture. Although rattlesnakes, like nearly all snakes, have only one functional lung, its capacity is relatively large, as the organ comprises not only a vascular section serving the usual purpose of aerating the blood, but a posterior smooth-surfaced extension, like a tubular balloon. This part increases the lung capacity, and hence lengthens the hiss on both inspiration and expiration.

It is to be remembered that snakes are deaf to air-borne sounds and that the hiss is a threat—a part of the defensive pattern—and not a means of communication between individuals. All sounds made by snakes, as far as known, including the rattle of the rattlesnake and the scale-scraping of the saw-scaled viper (*Echis carinatus*), are warnings;<sup>13</sup> for necessarily they must be made for their effects on creatures that can hear, which eliminates other snakes. Thus we may question the accuracy of the observation of Stradling (1882, p. 378), who heard a green snake (not a rattler) scream so that it was thought by passers-by to be the cry of a child. Some Brazilian natives believe that venomous snakes (including rattlesnakes) decoy small birds and mammals by imitating their calls (Fawcett, 1953, pp. 123, 251). Hudson (1893b, p. 456) tells of some harmless snakes that lived under his house and, while undisturbed, kept up a kind of hissing conversation.

Similar imaginary sounds have been imputed to rattlers, particularly the eastern diamondback (*C. adamanteus*). Allison (1946, p. 113) once bedeviled one until its hiss turned into growls. A friend of his saw a rattler coming down the trail with its mouth open, making a noise like the complaining of a distant bull. An-

<sup>12</sup> However, it would take keen ears to hear a bull snake at 30 yards or more, as Berridge alleges (1926, p. 24). He likens the sound to a bellow, which it certainly is not.

<sup>13</sup> I am referring to normal sounds, not such a noise as a sort of bubbling that has been heard to emanate from an injured snake when trying to hiss, or a sick one trying to breathe.

other saw one on the trail of a rabbit, weaving from side to side, and emitting a strange, humming moan. Meek (1946, pp. 19, 83, 103, 108, 134, 237, 244, 253) makes much of a mysterious mating call he attributes to the diamondback. The snake is smart enough to conceal this from all but a few human beings; when it knows men are about, the wailing call is changed to something like a bird's chirp. Stories of this kind usually emanate from sounds heard at night, when the source of the noise cannot be ascertained or identified. It may be pointed out that not only is there no evidence that rattlers make such sounds, but an anatomical examination fails to show a possible source.

Although a rattler usually hisses only while in the striking coil and when simultaneously rattling, this is not always the case. Sometimes it will stop rattling, yet continue to hiss. Veatch (1869, p. 151) noted that the Cedros Island diamond rattler (*C. exsul*) sometimes hissed when not sounding the rattle. A correspondent writes:

After climbing around the hills near Fontana, I sat down to rest. I heard a wheezing noise—something like the sound of a wind storm—off and on for about ten minutes or more, sounding as if it came from up the hill away, but to my surprise as I turned around, I saw a rattlesnake not 4 feet away. I watched it for about 15 minutes and it would make this noise as it expanded, and again as it would contract. C. W. Conkling, Los Angeles, Calif.

*Use of the Tongue.*—Another feature of the rattler's warning posture is the tongue, for a rattlesnake on the defensive uses this in a manner quite beyond the necessities of its function as a sense organ, and, in fact, even possibly interfering somewhat with that purpose. The rattler's tongue, like that of other snakes, is an adjunct to the sense of smell. As discussed in chapter 6 (p. 398), its tips serve to carry material particles secured in the air to the openings for Jacobson's organs in the roof of the mouth, from which the resulting responses are conveyed to the brain. When serving this purpose, the tongue is repeatedly flicked out horizontally, wavered slightly, and then retracted to make its depositary report. But a rattler on the defensive holds its tongue, extruded to the utmost, alternately vertically erect, and then downward, and this for considerable periods, 10 to 15 seconds or more, before retraction. The black tips are widely separated, and these, with the pink central column, make an imposing show, for they are the most mobile element in the entire posture. This use of the tongue seems to be primarily for its visual effect; for, although it is frequently withdrawn, the long pauses between retractions must actually interrupt, to some extent, the sensation of smell.

*The Scent Glands.*—Some items in the rattler's defense arsenal are used rarely and are not a part of the customary defensive posture. Most snakes are equipped with a pair of musk or scent glands in the tail. The discharges from these glands are not to be confused with those of the digestive tract, although they are sometimes emitted simultaneously when snakes are handled. The purpose of the glands is not known with certainty, and the use may differ in different kinds of snakes, although from the exceedingly offensive odor of the discharge in many genera—the garter snakes (*Thamnophis*), king snakes (*Lampropeltis*), and Nearctic boas (*Lichanura*),<sup>14</sup> for example—and the fact that they are excreted when the snakes

<sup>14</sup> With some practice one can recognize the different odors of some of the more nauseating genera. Elliot (1934a, p. 509) stated that he could distinguish cobra from Russell's viper scents.

are handled, it may be assumed that they comprise a defense mechanism. The glands in the female differ from those of the male, and it might be presumed that the scent would serve to bring the sexes together. However, Noble and Clausen (1936, p. 315) and Noble (1937, p. 720) found that these secretions played no part in sex recognition in *Thamnophis* and *Storeria*. Volsøe (1944, p. 50), on the other hand, is of the opinion that the glands may serve to attract the males to the females in the European vipers (*Vipera*). Fraser (1936-37, p. 279) even suggested that they might secrete a liquid necessary for the viability of sperm, but there is no evidence of such a purpose.

Whether the postanal scent glands of the rattlers serve any purpose in the mating pattern is not known, but at least it is evident that they are occasionally used as a part of the defense mechanism, especially if a snake is being handled or mistreated. Rattlesnake scent is to me pungent but not particularly offensive, much less so than the disgusting odors emitted by garter and king snakes, for example. However, some people consider it decidedly unpleasant. Thatcher (1940, p. 37) deemed the scent more objectionable than that of the skunk—certainly an exaggeration. As early as 1683, Tyson (p. 38) not only recognized the scent glands as such, but observed, as is true of many scents, that it was unpleasant when concentrated, but not so when diffused. This no doubt accounts for the differences in opinion as to the unpleasantness of the rattlesnake musk.

In the rattlers the discharge is a thick liquid, dark-brown in color; it is thinner than in many other snakes, in some of which it has the consistency of a jelly, and may vary in color from white through yellow to brown in the different genera. In the rattlers, as in most snakes, the glands are larger in the female than in the male.

As I have stated, a discharge from the glands is likely to be made when a snake is handled or frightened. An ejection from the glands is not unusual when a rattlesnake is being milked for venom, as I have often observed. I saw a young eastern diamondback (*C. adamanteus*) that was backing away in his defensive pose, suddenly emit two streams of musk in long, fine sprays. Later this was repeated when the snake was held in the hands. In another case, a young female southern Pacific rattler (*C. v. helleri*) that had been swallowed as far as the tail by a king snake, suddenly squirted out the contents of the scent glands. This snake, by the way, was far from being sexually mature. Discharges from the glands, in fact, may be squeezed from very young snakes, an argument against the interpretation of a sexual purpose of the glands.

William H. Stickel informed me of a large western diamond rattler—a male—that was shot in the neck with .22 dust shot. Although the head and neck were practically lifeless, the body and tail were capable of motion. In this condition, when the body was touched posteriorly, the snake ejected musk, and this was repeated 4 times, which shows that it was no accident. Ott (1882, p. 516) said he was often sprayed with musk while handling rattlers to test the speed of vibration of the rattle. Fitch (1949a, p. 518) has reported that he was frequently sprayed when pulling northern Pacific rattlers out of rocks by their tails. Thus we may definitely conclude that discharges of musk or scent from the postanal glands of rattlesnakes are used in defense, although they are not particularly effective. It is to be doubted whether these discharges—which are

seldom in evidence unless rattlers are held or restrained—are the source of the stories of the very strong odors given off by single rattlers or aggregations, whereby their presence can be detected for long distances. For these stories do not usually involve disturbed snakes, but rather, congregations such as are to be found at a den; they are discussed more fully under myths in chapter 18 (p. 1269).

*Body Flattening.*—One element of the defensive posture—the extreme flattening of the posterior part of the body—may be largely utilitarian, for it results in a more adequate base from which a strike may be launched. Also, the flattening is so marked that it seems to increase the apparent size of the snake and may thus serve to accentuate the threatening posture (fig. 2:57). It is more characteristic of a snake standing its ground than one retreating, while still facing the enemy in the striking coil.

That the flattening is, indeed, partly an intimidating pose may be judged from the fact that rattlesnakes striking prey do not flatten to anywhere near the same extent. Guided by the difference between the attitude toward an enemy and toward prey, we may distinguish between those features of the pose that are largely utilitarian, such as the S-shaped wave in the neck, and those that are a part of the pattern of intimidation, such as the rattle, the hiss, and the vertical tongue. For the latter are not a part of the posture preparatory to a strike for food.

The question may be asked whether rattlesnakes distinguish between different classes of animals and adopt different defense mechanisms to repel them. There can be no question that they do recognize king snakes and other ophiophagous enemies. The peculiar defense reaction employed against king snakes has been described elsewhere (p. 1102). No doubt rattlers can distinguish mammals from reptiles by use of their facial pits, but whether this induces a variation in the defense reaction is not known. Chalmers (1878, p. 422) reported that a dog would excite a rattler more than any other animal; and V., C.A. (1913, p. 498) tells of several people that passed close to a rattler without seeing it, although a dog detected it at once. From this he deduces that rattlers know instinctively that they can't escape detection by a dog and therefore rattle at once when one comes near. But Loennberg (1894, p. 335) saw a dog sniff a diamondback (*C. adamanteus*), which seemed to take no notice of it.

The pose adopted by the rattler in the so-called male dance, although it may have some elements of a defense posture, is discussed in chapter 10 (p. 703).

#### MYTHICAL DEFENSIVE ACTIONS

With creatures so provocative of sensationalism, it is not surprising that some rather fantastic stories have been printed concerning the defense reactions of rattlesnakes. Carver (1778, p. 480) reported that when a snake is animated by resentment, every tint rushes from its subcutaneous recess, giving the surface of the reptile a deeper color. Lacépède (1788–89, vol. 2, p. 395; Kerr, vol. 4, p. 250) said some reports alleged that the scales on the snake's back were erected when the reptile was enraged. Bartram (1791, p. 267) records that a disturbed snake bares its fangs, and the tongue becomes the color of the hottest flame. Ashe (1808, p. 142) tells of a rattler rearing its snout no less than 4 feet above its coils, with the head swelled to a violent degree, and its throat shining with beautiful

and vivid colors. Hill (1890, p. 194), writing in 1799, noted that a rattler's colors heightened surprisingly as it made ready for defense. Silliman (1820, p. 229) was told by his guide of a rattler that pursued a young man in a series of leaps; he thought this story sufficiently credible to warrant printing it.

The picture of a rattlesnake threatening an enemy with gaping mouth and protruding fangs is an ever-recurring one in the literature, but it is not true of an uninjured snake. Such stories gain credence from seeing a snake that has injured its mouth in striking something, or whose head has already been damaged by a blow. Such an account of a rattler threatening with open mouth is given by Daudin (1801-4, vol. 5, p. 302), Ker (1816, p. 20), and by Murray (1829, p. 316). The latter further reported that the whole body of the cornered snake rose and fell like a pair of bellows. This is an exaggeration of the inflation and deflation involved in hissing. Weston (1836, p. 167), Martin (1851, p. 271), Reid (1889, p. 230), and Carmer (1936, p. 319) repeat the open-mouth story. Parkman (1870, vol. 2, p. 265) speaks of the arched neck, the white fangs gleaming in the distended jaws, and the small eyes darting rays of unutterable fierceness—in all, a sacrifice of biological fact to literature. Beyer (1900, p. 30) mentions the ominous glitter in the eyes of an enraged *adamanteus*.

Although no species of rattlesnake is known to threaten with open mouth, some venomous snakes do so habitually, one of the best-known being the water moccasin (*Agkistrodon piscivorus*). Indeed, this is so characteristic of the species that it has earned it the name "cotton mouth" from the whiteness of the open mouth when threatening an enemy.

G. H. Wyman (1892, p. 588) tells of rattlers going a mile from their dens to make a combined attack on their enemies. In Arizona they raided a ranch house one night and drove out several sheepherders.

Lest we think that these myths and exaggerations could have been imposed only on the credulous authors of bygone days, we have Gibson (1940, p. 24) reviving the open-mouth story, and Meek (1946) promulgating a whole new series of fantastic yarns of the attacking methods used by diamondbacks: The man who was chased by a rattler and was searched for here and there as he hid behind a tree (p. 155); the theory that a rattler, sneaking away on the defensive, can shrink to half its normal length like a worm (p. 249); and finally the story of a man on horseback who was outrun by a diamondback (p. 262).

#### DISTINGUISHING THE RESTING FROM THE STRIKING COIL

One would expect no confusion between the resting and striking coils of a rattlesnake, for they are markedly different. But the fact remains that when some hunter, who has reported almost stepping on a rattler "coiled ready to strike," is asked to describe the creature's position, in nearly every instance he reveals that the rattler was in a flat, pancake-like coil—in other words, the snake was certainly resting and was probably asleep. For this motionless coil, this flat spiral of the body, with the head lying on the outer edge (fig. 7:1), is in notable contrast with the true striking coil. In the latter (figs. 7:2 and 7:3), the body is in a vertical spiral, with a widely opened loop as a base on the ground; above this, the anterior part of the body is erected, culminating with the head and neck in a loose S-shaped wave, like a poised and threatening lance. The striking coil

is in no way static—it is alive with motion, incipient or actual, a portent of disaster. For there is not only the wave in the neck that requires only straightening to produce a forward lunge—there are the other evidences of belligerence and menace: the sounding rattle; the hisses emanating from the swelling body; the flattened posterior affording a base from which the strike may be launched; and



Fig. 7:1. Southern Pacific rattlesnake (*C. v. helleri*) in resting coil.

the protruding tongue, alternately pendent and vertically erect, with the forked tips widespread. In this pose the snake well deserves Ruskin's descriptive phrase—an appearance of "malignant pride" (1875, p. 199). It is alert, hostile, and menacing. And back of the noise of rattle and hiss, the waving tongue and poised head, is the threat of the really dangerous strike. At such a time a rattler seems almost to deserve its reputation for malevolence.

To return for a moment to the resting coil: Except for the fact that the body rests on the ground in several turns of a flat spiral, there is no particular uniformity of the arrangement. The head and neck, more often taking the form of an S than the arc of a circle, generally rest on the other coils. The rattle is

sometimes at the outer edge of the coil, but more often sticks up near the center. There seems to be no constancy in the direction of the spiral; it may twist outward either clockwise or counterclockwise. In some species the resting coil is more often a two-story affair, that is, with a larger part of the anterior section of the body lying on top of the posterior; this is especially to be noted in the Neotropical rattlesnake (*C. durissus*) and the Lower California rattler (*C. enyo*).

A rattler can strike only a short distance from its resting coil—only the distance involved in straightening the S-shaped section of the neck. But in any case it will almost never do this, preferring, if disturbed, to throw itself first into its

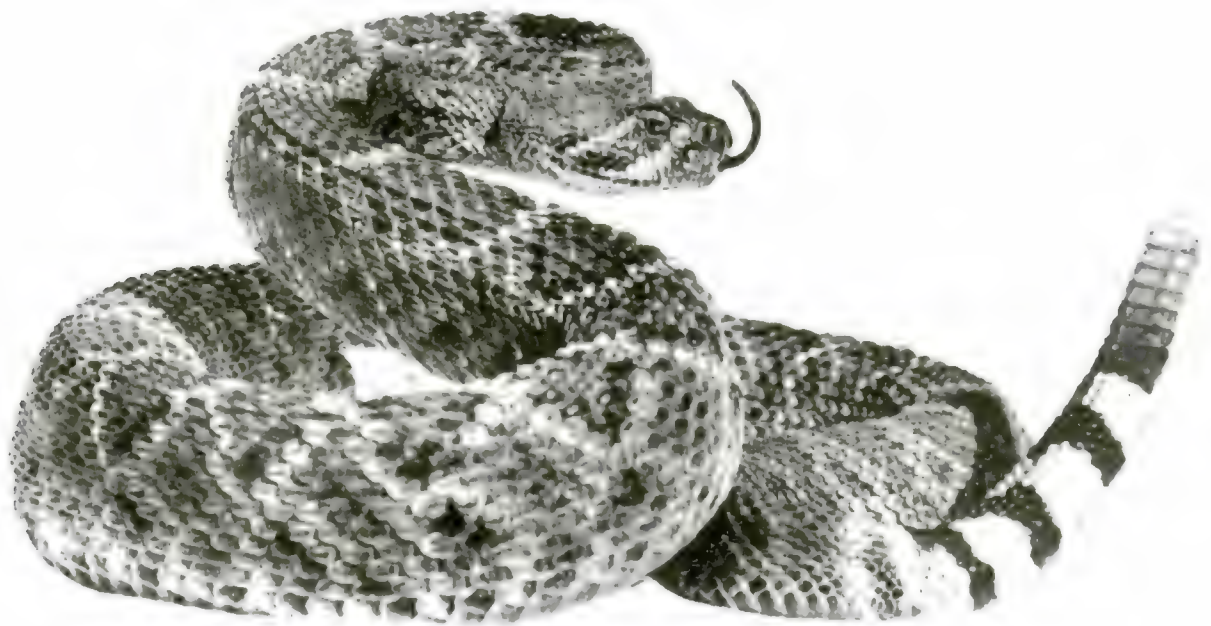


Fig. 7:2. Western diamond rattlesnake (*C. atrox*) in striking coil.

striking coil, which it can do very quickly by raising the anterior part of the body above the ground and at the same time spreading the after part into a wider loop to serve as an anchorage. Experiments with a piece of hose coiled to simulate a rattler in its resting coil will show that a forward lunge for any distance will twist the head laterally, thus illustrating the unsuitability of this type of coil for a strike. As Vorhies (1936a, p. 82) points out, anyone wishing to prove that a rattler in its resting coil is not "coiled ready to strike" has only to disturb one found in this position to note the quick change to the true striking posture. Crites (1952, p. 54) pointed out that a rattler is not so dangerous when coiled as when "gathered into folds," which was his way of describing the striking coil.

A rattler in its resting position will often be found settled down in grass or ferns as if they had been pushed aside to form a depression or bed. If rocks are nearby, a snake will usually coil with one edge of the body against a rock.

It is by no means unusual to find sidewinders (*C. cerastes*) bedded down in sand and partly covered over (fig. 7:4). They sink themselves into the sand by lateral undulatory movements of the body. The beds are sometimes in the open but more often under the protection of bushes. While sidewinders usually sink

themselves until flush with the sand surface, they apparently do not often intentionally cover themselves over, although not infrequently found partly covered by the drift. Ditmars (1923, p. 29) stated that a sidewinder, by flattening the body and making wavelike motions, could completely bury itself (except for the head)



Fig. 7:3. Southwestern speckled rattlesnake (*C. m. pyrrhus*) in striking coil.

in 15 seconds. While this may occasionally be done, it is doubted whether it is a normal method of concealment, although the marks in the sand made by the ventral plates show this to have been done by the snake in figure 7:4. Sidewinders are easily tracked on the desert in the morning before the wind comes up, and they are almost always found in the position described—that is, bedded down, but with the dorsum flush with the sand, rather than covered, although the outer coil, which has been used in making the bed, is often covered (Cowles, 1945, plate 1; Cowles and Bogert, 1944, plate 26). Some desert snakes do habitually cover

themselves completely, as, for example, the common sand and horned vipers of the Sahara (Pawlowsky, 1927, p. 279; Corkill, 1932b, p. 30; Mosauer, 1934, p. 59). The Saharan vipers show a more complete adaptation for an arenicolous existence in that their nostrils are equipped with valves to prevent the entrance of sand. Our sidewinders do not have such valves, but some of our southwestern desert snakes, such as the shovel-nosed snake (*Chionactis*) and the banded burrowing snake (*Chilomeniscus*), have them.



Fig. 7:1. Sidewinder bedded down in sand. The scale marks in the sand show that the snake used its neck to pull sand over its outer coils. (Photograph of *C. c. laterorepens* taken by Dr. Raymond B. Cowles, near La Quinta, Riverside County, California.)

The rattlesnake's striking coil is so characteristic, and the intentions of the snake so evident, that it attracted the attention of the early naturalists and is mentioned in such descriptions as those of Hernández (1615, fol. 192<sup>r</sup>; 1628, 1651, p. 328), Nieremberg (1635, p. 268), and Jonstonus (1653, p. 27). Dudley (1723, p. 293), Kalm (1752-53, p. 54), and others have pointed out that, as a rattler cannot strike unless suitably coiled, it is virtually harmless when outstretched. This is hardly true, since a rattler can bite in any position, and besides can assume a striking coil with great rapidity. Amaral (1927, p. 71) stated that rattlers usually coil with the left side of the body on the inside. I have not found this to be true of either the resting or striking coil.

From the standpoint of defense, the rattler's striking coil has several advantages over any other posture: The S-wave in the neck (a longer wave than the short

one of the resting coil) permits a forward lunge of the head without any lateral twisting that would disturb the sight or aim; the elevated position of the head permits a good view of the enemy, and the vertical section of the body allows a quick change in orientation; and, finally, the wide circle of the posterior part of the body not only provides a base from which a lancelike drive of the head may be launched, but likewise permits a retreat toward any available refuge while the snake still faces and threatens the enemy. A retreating snake faces backward, toward the enemy, across its own body, so that the length of the strike required to reach the foe is usually greater than in a snake standing its ground.

It should be understood that the striking coil of the rattlesnake is not unique; many other snakes, both venomous and harmless, adopt defensive postures that differ from that of the rattlesnakes in only unimportant details.

There is a widespread myth to the effect that rattlesnakes invariably coil clockwise in the Northern Hemisphere and counterclockwise in the Southern. There are also various beliefs as to the consistency with which the rattler, in its resting coil, has the rattle at the center of the coil or the periphery. But there is no uniformity in the position taken.

#### THE STRIKE

One of the best of the early descriptions of the strike of a rattlesnake was that of Gourley (1822, p. 186), who observed that the strike was only a forward lunge of the elevated head—a straightening out of the neck, the posterior part of the body remaining stationary.

The forward lunge of a rattlesnake from its striking coil, if it be thoroughly aroused, is delivered suddenly and with considerable speed—so fast, indeed, that the motion of the head cannot be followed with the eye. The withdrawal is slower and the motion can be observed. The snake does not threaten or start a strike with open mouth, but a glimpse of the open mouth can usually be faintly seen at the end of the stroke as the head reverses direction. Since the invention of high-speed motion pictures, it has been possible to photograph the rattler's strike so that the details of the mouth opening and the advancement of the fangs may be seen (Mili, 1946, p. 57; Van Riper, 1950, p. 128; 1953, p. 100; Van Riper *et al.*, 1952, p. 1). Four high-speed photographs of a rattlesnake's strike are shown in figures 12:1 to 12:4; these are from the Van Riper series. Further, by means of successive stroboscopic exposures taken of a striking rattlesnake, with a timing device in the background, Van Riper (1954, p. 579) was able to determine the speed of a rattlesnake's strike at the midpoint of the strike. It proved to be not nearly so fast as popularly supposed—far from the “fastest thing in nature” as has been stated. An adult prairie rattlesnake (*C. v. viridis*), in 20 separate tests, struck with an average speed of 8.12 feet per second (2.48 meters per second). The variation was from 5.2 to 11.6 feet per second (1.6 to 3.5 meters per second). There was some correlation of speed with temperature, although it was not high ( $r = 0.36$ ). These speeds are slower than those of a man striking with his fist. Further details of the nature of the strike were supplied by Van Riper in 1955 (p. 309). Recent experiments by Lester and Oliver (Lester, 1955, pp. 22, 116) indicate that *C. atrox* may strike faster than *C. v. viridis*. That temperature is important is indicated by the slowness of the strike at temperatures near the lower limit of rattlesnake

activity (see p. 390). Wood (1933, p. 85) tells of a prairie rattler that struck a thrown rock in mid-air. However, the stories of how rattlers unerringly strike bullets shot at them, so that it is impossible for a marksman to miss, are, of course, mythical (see p. 1262).

The rapidity with which a snake will repeat a strike depends on conditions, and particularly the continuance of the threat imposed. If the enemy does not retreat, a rattler may strike again and again at short intervals. Such a sequence was noted by Bailey (1876, p. 404), and is, indeed, not unusual. However, if the threat continues or the rattler misses several times, it may become cowed (Gibbs, 1892, p. 48).

A large rattler can strike with considerable force. Stone (1881, p. 473) tells of a man who was struck in a rubber boot between knee and hip; the blow felt like a thrown rock. In experimenting with fang penetration, I have caused large rattlers to strike objects such as shoes attached to a stick. The blow is a sharp one, but hardly sufficient to throw a person off balance as the Osages stated to Audubon (1827, p. 26).

The height at which a rattler's head is poised for a strike, depends, of course, on the size of the snake. A 4½-foot western diamond will strike from a height of about 8 to 10 inches and will lunge slightly downward. Puttees or other adequate protection below the knee will greatly reduce the danger in hikes through snake country.

Much has been written about the distance to which a rattlesnake can strike, which is also obviously dependent on the size of the snake. This is a matter of some practical importance since it defines the zone of danger. As a matter of fact, much depends on circumstances, such as the position of the snake, the species, and the degree of its excitement. There is, also a matter of definition involved, for, from what point should the length of the strike be measured—from the front, the center, or the back of the anchor coil on the ground from which the snake lashes out? Only in exceptional cases is it possible to determine the limiting point reached by the snake's head, the position of the snake's body when the strike was launched, or the length of the snake itself. Thus it is to be expected that the literature should contain many conflicting statements as to the distance a rattler can strike. Hogg (1928, p. 53) and MacDonald (1946, p. 135) give the maximum striking distance at  $\frac{1}{3}$  of the snake's length; Kalm (1752–53, p. 54), Carver (1779, p. 484), and Weld (1800, p. 409) at  $\frac{1}{2}$ ; Audubon (1827, p. 26) and Notestein (1905, p. 120) at  $\frac{2}{3}$ ; and, finally, Dudley (1723, p. 292), Oldmixon (1741, vol. 1, p. 188), Wesley (1784, vol. 2, p. 37), and Vigne (1832, p. 90) considered that a snake might strike up to its own length.

My own correspondents present somewhat the same ranges of observation:

When disturbed a rattler will flatten when coiled, rattle, then strike, I would say half its length. Some say a rattler will strike its full length, but not so here. *Gustave W. Koski, U. S. Fish and Wildlife Service, Windham, Mont.*



A 3-foot snake will strike sometimes a little better than a foot and a half. *Judge W. S. Owens, Cody, Wyo.*



I have never seen a rattlesnake strike over half of its length. *Albert Madarieta, Oakley, Idaho.*

A rattler can strike an object approximately at a distance of two-thirds of its length; thus one is safe when standing a yard away from a 3-foot snake. *A. C. Mackie, Vernon, B. C.*



As a matter of personal observation, I have seen a snake jump its full length in a strike. *H. P. Struble, U. S. Forest Service, Sonora, Calif.*

From my own experience I should say that a rattler will rarely strike more than half its length, measured from the front of the anchor coil, and almost never beyond  $\frac{3}{4}$  of that length. However, I should not like anyone to take this as a guarantee of safety, if only for the reason that one cannot accurately judge the length of a coiled snake.

One condition that affects the length of the strike is the nature of the ground. Bailey (1876, p. 404) believed a snake could strike  $\frac{1}{2}$  its length on the level, but 3 times its length downhill. K., A. (1905, p. 354) claimed to have noted strikes exceeding the snake's length with a favorable tail brace and a downhill slope. Stickel (1952, p. 12) believes that a rattler might strike for its full length if the tail were braced against something solid. Finney (1931, p. 9) says that a rattler can strike hard enough to slide the body forward somewhat; this could well be possible on a smooth surface and with a back-stop to brace against during the forward lunge. Dr. R. B. Cowles told me that he was always skeptical of stories of rattlesnakes leaving the ground in the course of a strike, until he saw this done two or three times by an angry southwestern speckled rattler (*C. m. pyrrhus*). The snake was on pavement and struck for more than its full length. Beck (1952, p. 145) reports, as an item of Virginia folklore, a belief that rattlers can leap through the air. Teale (1915, p. 124) was told that rattlers can strike twice as far backward as forward.

Some particular cases of long strikes are the following; Allen Kelly (1909a, p. 51) reports:

Dr. John Day and myself ascertained by actual trial 18 years ago that under some circumstances a rattler can strike the full distance of his own length and a little more. Dr. Day carefully observed the exact position of a small rattler's tail while I provoked the snake to strike my boot. With its tail against a clod and with a downhill line of attack, the snake, when aroused to almost frantic belligerency, struck my boot at a distance from the tail-site of two inches more than its total length as measured carefully by both of us.

Another rattler, a big, fat fellow, once struck at me from a bank on a trail in Calaveras, and although I was considerably further from his tail-hold than his total length, he managed to project himself off the bank, hit the brim of my hat and fall upon the trail.

Dixon (1926, p. 274) tells of a northern Pacific rattler that struck at his shadow, reaching out for nearly its entire length. Only about 4 inches of the snake's body remained in contact with the ground.

Anon. (1930a, p. 3) tells of a western diamond (*C. atrox*) at the St. Louis Zoo that made a lunge from a ledge of rock as the keeper was raking near him. The snake's strike was found to measure 5 feet, the length of the snake itself being 6 feet 4 inches.

Although rattlers in their striking coils usually strike on the horizontal or slightly downward, if the target be a large one, so that they need not aim at a particular spot, they can strike directly upward, or at any angle between. A vertical strike rarely exceeds a foot or foot and a half, even though the snake be a large one.

However, Watt and Pollard (1954, p. 368) describe the strike of a six-foot *adaman-teus* that lunged upward at a 45-degree angle and bit a man in the leg 22 inches above the ground, unfortunately above the top of the victim's snake-proof boots. Some collectors have believed that it is safe to seize a rattler by the neck from directly above because it was thought that a rattler could neither see nor strike directly upward. There is no truth in this supposition. The nature of the striking coil permits a snake to change quickly the direction of the strike to either side, upward, or even backward, should the enemy change his attacking position. Van Riper (1955, p. 311) has shown a stroboscopic photograph of a rattler striking straight upward.

There are some species differences in the rattlesnake's striking posture. Particularly, the Neotropical rattlesnake (*C. durissus*) is noted for its peculiar pose, in that the part of the body above the ground is held in an almost vertical column, with only a small crook at the neck (fig. 7:5). It is to be presumed from this position that these rattlers are likely to strike somewhat higher than do those inhabiting the United States.

The sidewinder has the reputation for making sidewise strikes without coiling (Mosauer, 1935c, p. 33; *American Guide Series, Nevada*, 1940, p. 20; Blackford, 1946, p. 10; Herrick, 1953, p. 23). It is true that the sidewinding method of progression facilitates rapid motion while the snake has the anterior part of the body raised for striking. Mosauer (1935c, p. 33) says the strike is often unexpected and is a sort of snap. He saw one strike so hard that the entire body seemed to leave the ground for an instant.

This brings up a point that has been a frequent source of controversy in the sporting and nature magazines—namely, whether a rattlesnake can strike without coiling. As is so often the case, the argument really stems from a misunderstanding or confusion of terms. Some persons seem to consider the terms "bite" and "strike" synonymous, which they are not. A snake, to bite, needs only to open its mouth and imbed its fangs in any object within reach. The muscular power of the jaws is quite sufficient to drive the fangs into tissue without the momentum of a strike, as many a man has learned to his cost when holding a rattlesnake behind the head so carelessly as to permit the snake to free an inch or so of neck and thus turn its head and reach its captor's hand. No strike is here involved, if, by strike, we mean a forward lunge of the head permitting a snake to reach an object that would otherwise be beyond its range. It is true that the momentum of a strike does aid in imbedding the fangs, which point almost directly forward as the head reaches the end of the stroke, but the strike is not an essential part of a bite.

Another source of dispute lies in a misunderstanding of the nature of the snake's coil. To many the word implies a flat, tight, pancake-like spiral—that is, the resting coil. Seeing a snake strike from other than this type of coil—and it would be impossible to strike more than a few inches from one—the observer says that the snake struck without coiling. But in almost every instance the snake has indeed struck from its typical striking coil—the open anchor loop, elevated forebody, and S-shaped crook in the neck—although this may seem to the observer to be too loose or open a formation to deserve the term "coil" at all.

But, aside from these arguments that flow from a lack of agreement upon definitions, it is true that rattlesnakes sometimes strike without the formality of coiling,



Fig. 7:5. Central American rattlesnake (*C. d. durissus*) in threatening pose. (Photograph by Dr. C. Picado T.; used through the courtesy of the R. L. Ditmars estate.)

or possibly it should be said that they pass in a single violent movement from a stretched-out position, through the striking posture, into the strike itself. For example:

June 30th of this year, I stepped on a rattlesnake and he struck my heel where I hit him. Another time I saw one lying stretched out in the road. I tried to stamp on his head, but he struck the side of my foot; he was that much quicker than I was. *Paul D. Wilcox, State Fish Warden, Wyalusing, Pa.*

Among the published accounts bearing on this point are those of Banks (1896, p. 144), who caused a horse to step over an outstretched rattler and later found that the horse had been bitten in the off hind fetlock. K., A. (1905, p. 354) claimed to have seen rattlers strike without coiling. McGuire (1930, p. 93) saw an outstretched rattler swing half its body around in a sweeping circle to strike without coiling.

From these accounts we pass to those that are to be considered quite beyond the realm of possibility. Martin (1851, p. 198) says a rattler jumps as a coiled spring would when compressed and released. Wilhelm (1873, p. 353) tells of a guide who aimed a sword cut at a 6-foot rattler. The sword missed and the rattler jumped over the man's arm and lit 8 feet beyond. Ellzey (1893, p. 25) claims a diamondback is so active that it could strike between the eyes of a man standing erect. Gibson (1940, p. 25) has seen rattlers launch themselves through the air and strike a foot beyond their lengths. All of these are capped by Meek (1946), who tells of the diamondback that struck double its length by diving across its own tail (p. 158);<sup>15</sup> the rattler that struck past a man 10 feet away, just missing him; another that struck and reached the knee of a man on horseback; another that just missed a horse's nose, to do which he leaped at least 8 feet clear of the ground; and finally the account of the snake uncovered in a hole that jumped 3 feet straight up out of the ground (p. 160).

The object of the strike is, of course, to bite—to inject venom into—the object of the snake's displeasure or appetite. This bite and its results are discussed in chapter 12.

### CLIMBING PROCLIVITIES

Whether rattlesnakes climb trees is a question often appearing in the queries columns of the sports and nature magazines. From the observations of many field men it is now known that they do so occasionally, but they are not as adept climbers as many other normally ground-inhabiting forms such as the rat snakes (*Elaphe*), the king snakes (*Lampropeltis*), the gopher or bull snakes (*Pituophis*), or the racers and whip snakes (*Coluber* and *Masticophis*), all of which frequently climb trees in search of birds and their nests. The rattler is handicapped in climbing by its relatively stout body and short tail; it cannot climb with the facility of the more slender-bodied snakes. Many true tree snakes are notably attenuated, *Oxybelis* and *Imantodes*, for example, although others, such as the boa constrictor, are quite thick-bodied. Some climbers have the advantage of prehensile tails or other modifications that adapt them for climbing.

In the zoo, rattlers occasionally climb the small shrubs in their cages, but do not remain there at rest for long periods as do many of the other snakes. Possibly they may climb to find some avenue of escape. At any rate, it is presumed that in the wild they usually climb in search of food, rather than to seek places of refuge.

It may be thought that some species of rattlers are more likely to climb than others, and this may be true, the timber and black-tailed rattlesnakes being among the more persistent climbers. Yet the following observations, segregated by species,

<sup>15</sup> A retreating rattler may strike across its own tail, but not twice its full length.

show how widely prevalent the custom is, for nearly every species common enough to be under frequent observation has been observed upon some occasion up in a tree or bush.

*Eastern Diamond Rattlesnake (C. adamanteus)*

On March 16, 1911, I was walking through a thick piece of woodland on Prospect Hill. I observed an unusually large diamondback rattlesnake (*Crotalus adamanteus*) coiled in a wax myrtle tree between 10 and 12 feet from the ground, immediately under a large wood-rat nest. I presumed the snake was in the tree for the purpose of getting a meal of the rats. E. A. McIlhenny, Avery Island, La.

As to published *adamanteus* records, Lovejoy (1881, p. 347) states that he found one of this species up in a large water oak with water all around the base of the tree; the snake was about 30 feet above the water, stretched along a limb some 10 feet out from the trunk. It was a large snake about 6 feet long. The tree was leaning at an angle of 15 degrees. Another was seen in the top of a fallen tree on a limb about 10 feet above ground.

Rutledge (1936, p. 138) reports a diamondback 15 feet up in a tree. No bird's nest that it might be seeking was to be seen. But on another occasion he found a diamondback in a woodpecker's nest in a tree; the snake had eaten a woodpecker and several eggs.

*Western Diamond Rattlesnake (C. atrox)*

On March 15, 1944, about 22 miles southwest of Falfurrias, Brooks County, Texas, I found a rattlesnake stretched out along a mesquite limb about 3 feet above the ground. Upon my approach, the snake crawled across to another branch, but made no attempt to descend until I struck it with a stick. I saw no evidence of any prey in the bush, and no other reason for the snake's presence there. W. C. Glazener, Wildlife Biologist, Falfurrias, Tex.



I have never seen a rattler in a tree, but I did find a very small one, resting on top of a weed stalk about a foot high. It was sprawled about on the top of the weed. A. J. Kirn, Somerset, Tex.

O. D. Herron, of Mohawk, Arizona, told me of finding a western diamond stretched on a limb several feet up in a mesquite. Dobie (1945) reports rattlers of this species seen 3 or 4 feet up in prickly pear cactus.

*Sidewinder (C. cerastes)*

On May 15, 1945, I encountered a sidewinder in Red Rock Canyon, at the south end of the Charleston Mountains, about 20 miles west of Las Vegas, Nevada. As I desired to secure a Kodachrome picture of him, I poked the snake out of a small hole and he immediately crawled into a small bush about a foot or so in height. He remained there for some few minutes and then crawled into an adjacent bush a little higher, and from there to the ground. Gordon C. Baldwin, Boulder Dam National Recreational Area, Boulder City, Nev.

Dannaldson (1938, p. 7) found a sidewinder up in a mesquite.

*Lower California Rattlesnake (C. e. enyo)*

When setting my line of mouse traps near Cataviña, Baja California, I ran onto a small rattlesnake up in a *Franseria* bush, perhaps 30 inches above the ground. I collected the snake which was later identified as *Crotalus enyo*. L. M. Huey, San Diego Society of Natural History, San Diego, Calif.

*Timber and Canebrake Rattlesnakes (C. horridus)*

On March 29, 1894, I was trying to shoot a couple of crows that had a nest in a large double-stemmed water oak. The trunk was single up to about 10 feet above the ground. When I got near the base of the tree, I noticed that the crotch was broad, and upon looking more closely saw, coiled in the crotch where the two stems met, a full-grown canebrake rattlesnake (*Crotalus horridus atricaudatus*). This snake was coiled in a natural manner, and was evidently resting. *E. A. McIlhenny, Avery Island, La.*



Just last month, while marking timber at an elevation of 4,300 feet, I encountered for the first time a climbing rattlesnake. It was coiled in the bushes approximately 3½ feet above the ground in blackberry briars. *C. R. Carr, U. S. Forest Service, Richwood, W. Va.*



In the Cabin Creek Mountains of West Virginia, I have seen many timber rattlers. The only one off the ground was in the top of a fallen chestnut oak, about 6 or 7 feet from the ground. A wood thrush nearby was complaining. Upon my approach, the snake slid to the ground and disappeared in the dead top. *Josiah Keely, Huntington, N. Y.*



In the two cases that I recall seeing rattlers up on the limbs of trees, they, so far as I know, were not after birds or birds' eggs, but merely sunning themselves. However, the studies that were made on this forest a few years ago indicate that the diet of rattlesnakes is made up of about 12 per cent birds and eggs, which would suggest that they would climb up to get this food. *Abner Casey, U. S. Forest Service, Bridgewater, Va.*



One evening, at twilight in October, I observed a rattlesnake lying on a bush about 5 feet off the ground. I imagine it was after birds. There was nothing in its stomach. *W. H. Britton, Chambersburg, Pa.*



I witnessed a unique escape of a rattler (*C. h. horridus*) when disturbed at a den. Two rattlers were coiled on a stump about a foot high. When I noosed one, the other, instead of taking refuge in the jumble of rocks round about, chose to climb rather heavily upward via a tangle of greenbrier vines into a birch tree that was laced with the vines. The snake disappeared in thick foliage about 10 feet above the ground. *Stephen H. Harwig, Pittsburgh, Pa.*

Among the published reports of the tree-climbing proclivities of this snake are those of Abbott (1873, p. 433), who found one roosting in the branches of a slanting oak tree; Palmer (1887, p. 343), who came upon one in a tree while coon hunting; Linsdale (1927, p. 80), who shot two out of trees at heights of 15 and 6 feet above ground; MacQuarrie (1911, p. 83), who was told by the well-known collector, Elmer Keitel, that this species is occasionally found in trees in Wisconsin; and Anderson (1951, p. 6), who reported one 4 feet above ground in blackberry bushes.

Of these reports on the climbing proclivities of *C. horridus*, those by McIlhenny and Spiller refer to the subspecies *C. h. atricaudatus*, the canebrake rattler; the others refer to *C. h. horridus*, the timber rattlesnake, or are indeterminate.

*Speckled Rattlesnake (C. mitchelli)*

The only rattler I ever saw in a bush was a speckled rattler (*C. m. pyrrhus*) that climbed up about 3 feet when I frightened it. *Frank F. Gander, Escondido, Calif.*

Winfield H. Line, of Palm Springs, told me of having seen a rattlesnake of this subspecies—a colored photograph left no doubt as to its identity—in wild grapevines about 18 inches above a stream bed.

Bendire (1881, p. 207) records having found a rattler near Owens Lake, 2½ feet up in a bush. This was probably a Panamint rattlesnake (*C. m. stephensi*), a subspecies of the speckled rattler.

#### *Black-Tailed Rattlesnake (C. molossus)*

A 30-inch northern black-tailed rattlesnake was taken in a hackberry tree along the visitor trail in the creek bottom, here at the Monument. The snake was about 7 feet from the ground and handled itself quite well as it moved from branch to branch. It was difficult to see because it blended so well with the foliage. A visitor was walking along the trail and discovered it when it rattled as he was passing. Although I could find no squirrel or bird's nest in the tree, I suppose it was looking for food. *Homer F. Hastings, Camp Verde, Ariz. (Quoted from observations recorded by Ranger Robert S. Leding, Montezuma Castle National Monument.)*



The only rattler I ever saw in a tree was a blacktail. It was in an advantageous position for capturing the lizards that were constantly running up and down the trunk. *Paul V. Woolley, Jr., University of Kansas, Lawrence, Kans.*



A rattlesnake (later identified as a blacktail) was shot in a cedar tree at my Cedar Oaks summer home. The snake was coiled amid the branches about 9 feet above the ground. The tree trunk was free of branches 5 feet from the ground. *Peter P. Hoefgin.*

The account of this incident was sent me by Col. M. L. Crimmins, of San Antonio, who states further that captive snakes of this species frequent the limbs of bushes placed in their cage. In another report from Col. Crimmins, he mentioned a *molossus*, also nine feet above ground, but this time in a mesquite tree.

Allen (1933, p. 15) reported two blacktails found in bushes about six feet above ground.

#### *Red Diamond Rattlesnake (C. r. ruber)*

One night at about 10:30 I was returning with a companion to my home in Suncrest, San Diego County. The trail ran through a patch of buckwheat (*Eriogonum*). While walking through this patch, we heard a slight scraping or clicking sound, much as though a rattlesnake's rattle was being dragged over the brush. Fortunately, we had a flashlight which we turned in the direction of the sound, and there, stretched through the tops of the buckwheat bushes, about 2½ or 3 feet off the ground, was a red diamond rattler (*C. r. ruber*), 30 inches long. Just what he was doing up there, I don't know. There was no bird's nest in his immediate vicinity that we could see, nor any pack-rat (*Neotoma*) nests, either. *Charles E. Shaw, San Diego Zoo, San Diego, Calif.*



Though the red diamond rattler is generally found on the ground, I have on occasions found them in trees or brush. For instance, a year ago I found a small female lying stretched out full-length, at least six feet above ground on the limb of a sumac bush. Another time I found a female under similar conditions in a tree, while on the ground beneath lay a large male, outstretched. Then several times I have found both sexes on the top branches of cactus five feet high, some coiled and some stretched out. *Louis P. Faldborg, Chula Vista, Calif.*

I myself found a red diamond rattler in a bush about 18 inches above the ground. I had stopped by the roadside to follow a crossing track and located the snake about 20 feet off the highway. It tried to escape by crawling through the bushes, still at a height of about a foot or so above ground. On another occasion I found a snake of this species off the ground in prickly pear cactus.

*Tiger Rattlesnake* (*C. tigris*).—R. R. Humphrey, of the Desert Laboratory at Tucson, told me of finding two tiger rattlesnakes at about 7 P.M., in Sabino Canyon; one was in a bush about 2 feet above ground, the other under a rock.

*Western Rattlesnake* (*C. viridis*).—Because of the extensive observations available on the western rattlesnake, the subspecies are treated separately.

*Prairie Rattlesnake* (*C. v. viridis*)

Some people say a rattler will not climb trees; however, a number of years ago my wife and some of our friends were having a picnic on the bank of Rattlesnake Creek, twelve miles from Cody. While eating our lunch in the shade of a large cottonwood tree, one of the party in looking up discovered a large prairie rattlesnake dangling from a hole in the trunk of the tree at least 25 feet above ground. I should say that this hole was made by a woodpecker and it may have had young birds in it. The tree had a slight lean to it but even so it looked impossible for the snake to climb. *Judge W. S. Owens, Cody, Wyo.*



I saw a rattler climb a tree once, but the tree was at a slope of some 25 or 30 degrees. *William Lakanen, Game Warden, Rawlins, Wyo.*

*Coronado Island Rattlesnake* (*C. v. caliginis*).—Nelson K. Carpenter found a rattler of this subspecies on South Coronado Island (the only place where it occurs) coiled on the top of a thick bush about 3 feet off the ground.

*Midget Faded Rattlesnake* (*C. v. decolor*)

B. W. Allred of our Service informed me that on a cool October day at Moab, Utah, he found a rattlesnake stretched along the limb of a peach tree about 3 or 4 feet from the ground. He thought it was probably sunning itself. *Philip F. Allan, Soil Conservation Service, Fort Worth, Tex.*



I used to live on the Green River in Utah and I remember on one occasion seeing a rattlesnake up in a squaw bush about 6 feet from the ground. What it was doing there, I could not say, but I suppose it was hunting for a bird's nest. *Leonard Slauch, Game Warden, Mack, Colo.*

*Southern Pacific Rattlesnake* (*C. v. helleri*).—Mrs. Griffing Bancroft, on September 30, 1945, found a young *helleri* about 20 inches above ground on the bole of a large buttressed post oak at Witch Creek, San Diego County, California.

According to a newspaper report, a rattlesnake of this subspecies about 3½ feet long was found ensconced in the crotch of an oak tree, 14 feet above ground. This was in Laurel Canyon, north of Hollywood, Los Angeles County, California, August 7, 1946.

*Great Basin Rattlesnake* (*C. v. lutosus*).—Linsdale (1940, p. 252) reported finding a rattler of this subspecies in a bush 2 feet above ground.

I found a rattlesnake up in a cedar tree, about 7 feet off the ground. It was after a robin's nest that had young birds in it. *Ollie Cox, U. S. Fish and Wildlife Service, Eureka, Nev.*

*Northern Pacific Rattlesnake* (*C. v. oreganus*)

Rattlers will climb up in blackberry bushes and grape vines, apple trees and all kinds of bushes, to hide and wait for birds. *Marion E. Rose, Pateros, Wash.*

I have seen only one rattler in a tree. It was in a woodpecker hole and had devoured six little ones. I was attracted by the old one fussing at the snake. *Lawrence Kelly, Harper, Oreg.*



One of our science teachers, who has lived in the northern end of Butte County, on occasion has observed rattlesnakes up in the shrubbery, sometimes as high as 3 feet. In fact, she said she had had them flee from her up into the bushes. *Esther L. Guthrie, Supervisor of Science, City Schools, Sacramento, Calif.*

Dr. William F. Bade told me of watching a Pacific rattlesnake in the Sierra climb a small aspen tree some 3 or 4 inches in diameter, and then saw it stretch out on a branch some 15 feet above ground.

Bendire (1881, p. 207) reports having seen Pacific rattlesnakes in willows as high as 5 feet above ground.

#### *Western Pigmy Rattlesnake (S. m. streckeri)*

I have observed the pigmy rattler on a limb of a blackjack tree about 26 feet from the ground. *Harold C. Nygren, U. S. Forest Service, Winona, Mo.*

*Miscellaneous Accounts of Tree-Climbing Rattlesnakes.*—Some published accounts of tree-climbing by rattlesnakes wherein the species cannot be determined with certainty, include Sass (1935, p. 250), Tixier (1940, p. 77), Benton (1945, p. 80), and Manu (1947, p. 53).

Several reports of tree-climbing rattlesnakes received from my correspondents also concern indeterminate species:

On another occasion I found a small grey rattler in the forks of a small oak tree. This was in the mountains of this state, at an elevation of around 6,000 feet. *Riley Millegan, Silver City, N. Mex.*



With Deputy Game Warden George W. Peterson, I was searching for white-winged dove nests in the oak-grown canyons opening into Sonoita Creek west of Patagonia, Arizona. Walking under each oak tree looking upward for nests, I discovered a coiled snake, on the side of a large branch, where several twigs made a flat, shelf-like arrangement. Using the sectioned mirror-pole we used to inspect nests, which was 12 feet long, the snake was found to be 12 feet 4 inches from the ground. The snake measured 31 inches; it was a pretty rattler, medium to dark green in color, without any specially distinct striping of any sort; it had seven rattles and a button.

We spent 20 minutes studying the tree and the place where the snake had been coiled, and I still have no idea as to how this relatively short and heavy snake could have climbed the tree. There were no twigs or side branches short of 8 feet from the ground. From the perpendicular, the trunk did not lean more than 5°. Climbing the bare trunk by looping and clinging to the rough bark hardly seemed possible for this snake; yet there it was.

We inquired of cowboys and woodsmen in that locality, and none had ever seen a rattler so high; several stated that a greenish rattlesnake in that area had often been seen climbing about in low brush, as though in search of birds' nests. *Johnson A. Neff, U. S. Fish and Wildlife Service, Albuquerque, N. Mex.*

There are two greenish rattlesnakes found in the vicinity of Patagonia, Arizona—the northern blacktail (*C. m. molossus*) and the Mojave rattler (*C. s. scutulatus*). The blacktail is known to climb, field observations to this effect having already been cited; I have no records of climbing by the Mojave, although it may do so.

I have found rattlesnakes coiled in the tops of sage brush seeking young birds or bird eggs. *Charles H. Nugent, U. S. Fish and Wildlife Service, Brawley, Calif.*



I have seen rattlers up in bushes twice; once in a *Simmondsia californica* bush in White-water Canyon on the Colorado Desert, and once at Palm Springs in a "deer-mouse" cactus (*Opuntia echinocarpa*). In both cases there were nests of the desert black-throated sparrow containing young in the bushes. This was in April, 1916. *E. C. Jaeger, Riverside Junior College, Riverside, Calif.*

#### REASONS FOR TREE-CLIMBING

Various reasons have been advanced to account for tree-climbing by rattlers; most observers believe it is for the purpose of securing food. Bendire (1887, p. 304) thought they would climb if small mammals, birds, or eggs were to be had. He mentioned one instance in which a rattler was found coiled around a nest 15 feet above ground.

Some observers report that rattlers occasionally climb into bushes to avoid water or to dry themselves:

I have seen rattlers on bushes several feet high, drying after a rain storm. *Frank E. Brink, Fish Warden, Milford, Pa.*



I have observed rattlers resting on brush. I think they were seeking the warmth of the sun. *Emmett Wilson, Pensacola, N. C.*



When water covers the land, rattlesnakes sometimes go up in bushes. If they are disturbed and forced to come down, they become angry. *Charles W. Coffin, Holly Bluff, Miss.*



When the heavy rains come, the water covers hundreds of acres of swale land, to a depth of a foot or 15 inches, and the snakes and rats all have to climb trees, or brush, or go into the big rat houses that they built for the purpose. I've seen rattlers climb trees, and also knocked them out and watched them swim. *Dow Jones, District Game Warden, Palisade, Colo.*



I have seen many rattlesnakes crawl up in clumps of sage brush when it was raining and wet on the ground. They would be on sage brush clumps about 10 to 16 inches above the ground. They would crawl up there to get out of the mud. *Eddie Buchta, U. S. Fish and Wildlife Service, Moneta, Wyo.*



Rattlesnakes will try to avoid water under some conditions. Several years ago, during a flood in one of my stock pastures, I saw a rattlesnake in a hackberry tree, up about 4 feet from the ground, which was flooded. *A. L. Alexander, U. S. Forest Service, Roosevelt, Ariz.*

Carr (1940, p. 95) states that, when the Everglades are flooded, the pigmy rattlers (*S. m. barbouri*) are often seen in small trees, or lying coiled on cabbage-palm leaves 8 or 10 feet high.

One observer advances another reason for their climbing:

I have seen several rattlers halfway up a sage brush. The purpose, I think, was to keep from being trampled by a band of sheep which I was driving at the time. *Albert Madarieta, Oakley, Idaho.*

On the distinctly mythical side we have G. A. Fitch (1903, p. 315) maintaining that rattlers in northern California catch insectivorous birds by imitating the buzzing of a bee with their rattles. He saw this done by rattlers concealed in the dense foliage of trees 20 feet above ground.

Some think their climbing is not so much to search for birds' nests as for the purpose of finding an advantageous perch for spying prey or enemies:

I have seen a rattler climb up in the fork of a mesquite bush and coil up there waiting for his prey to come by. He can strike very effectively that way. I have watched them catch small rabbits, mice, and small squirrels. *Riley R. Osborn, Game Warden, Torrey, Utah.*



I have seen rattlers on top of bushes 3 or 4 feet high, but never knew what their purpose was in going there unless to get away from some danger. *Walter F. Emerick, Division of Fish and Game, Palmdale, Calif.*

Various observers have seen rattlers ensconced on or climbing objects other than trees or bushes. E. A. Schilling, U. S. Forest Service, Franklin, Pennsylvania, found a timber rattler crawling along the second rail of a rail fence. Homer F. Hastings, National Park Service, Camp Verde, Arizona, saw a 37-inch blacktail attempting to climb a stone wall. G. W. Danforth advised me that at the weather station on Mt. St. Helena, near Napa, California, a small northern Pacific rattler was found in a latticed box that held the station thermometer. The box was mounted on a post and it was difficult to see how the snake could have climbed into it.

Among published records, Abert (1831, p. 221) mentions rattlers on the top rails of fences. This is repeated by Bachman (1834, p. 164; see also Herrick, 1917, pp. 53, 64).

#### CONTROVERSIES CONCERNING TREE-CLIMBING

In the early days, naturalists both affirmed and denied that rattlesnakes climb trees. When the belief in the power of fascination was at its height, it was thought the snakes had only to fix their baleful eyes upon some unfortunate bird or squirrel, whereupon the helpless prey fluttered or fell into the waiting mouth below. Hence it was unnecessary for the snakes to exert themselves to climb trees. But Lacépède in 1789 (p. 409; Kerr, vol. 4, p. 263) stated that they did climb trees. Barton (1799, p. 103) wrote that they seldom climbed, at least to any great height. But Martin (1851?, p. 271) insists they never climb trees.

About a century ago there raged a bitter controversy involving John James Audubon, the American artist-ornithologist and Charles Waterton, the British traveler and naturalist. The controversy on Audubon's side was carried on by his son, his friends, and supporters, for it appears that Audubon rarely replied to his critics, except in letters to his friends (Brewer, 1880, p. 671; Herrick, 1917, p. 64).

The discussion was centered principally on the accuracy of Audubon's plates and descriptions; and since the disputed points were mostly ornithological they need not be considered here.<sup>10</sup> But Waterton also criticized Audubon's discussion of rattlesnake habits, and in this he had the better of the argument. It is

<sup>10</sup> Those who are interested may consult the *Magazine of Natural History* from 1830 to 1835. Here they will find the shots fired by both sides, or appropriate abstracts from, and references to, items appearing in other journals. See vol. 3, p. 449; vol. 5, pp. 233-241; vol. 6, pp. 83-88, 162-171, 215-218, 369-372, 464-468, 550-553; vol. 7, pp. 66-74, 164-175, 276-283; vol. 8, pp. 184-192, 540-541, 663-667. See also the works on Audubon by Herrick (1917, vol. 2, pp. 61, 68, 71), Rourke (1936, pp. 170, 239), and Arthur (1937, p. 216); likewise *Audubon's Journals* (Maria R. Audubon, 1917, vol. 1, pp. 211, 213).

evident that Audubon confused his observations on rattlesnakes with others on black snakes, and he was not insusceptible to repeating herpetological myth and folklore.

The rattlesnake part of the controversy began with the publication of Audubon's famous plate No. 21,<sup>17</sup> showing a timber rattlesnake in a tree threatening a mockingbird's nest, which is being defended by the parents and another adult bird. This was followed by an article on rattlesnakes (Audubon, 1827). Criticism of the plate was centered on the rattler's presence in the tree, and also on the recurved shape of the fangs, which are visible, for the rattler is threatening the birds with open mouth, in itself highly improbable, to put it mildly. The fangs—two per side—are much more recurved than any of the many hundreds I have examined, and the pterygoid teeth are exaggerated in size. Although a slight reverse curvature in rattlesnake fangs at the points is by no means uncommon, particularly when dried, Audubon has shown a reverse curvature at the approximate centers of the fangs. It can hardly be claimed that this plate enhances Audubon's reputation for accuracy of detail, although one cannot take exception to the major premise of a rattler raiding a mocker's nest. But the published article leaves even more to be desired; it is replete with repetitions of folklore, including the boot myth (see p. 1281), and inaccurate observations. It is much inferior to other accounts of the rattlesnake that had appeared previously. As far as climbing trees is concerned, Audubon stated that he had seen a rattler pursue a gray squirrel on the ground and gain on it (p. 22). The rattler then chased the squirrel up a tree, and from branch to branch, bridging gaps with  $\frac{2}{3}$  of its body when necessary. Finally the snake caught the squirrel and killed it by constriction. All of this might have been true of a black snake; almost none of it could be true of a rattler. No rattler could outdistance a squirrel, either on the ground or in a tree; it could climb a tree only slowly and with difficulty; with its heavy body and almost useless tail, it could not bridge the gaps between branches as stated; and finally it would not kill a squirrel by constriction.

Audubon's paper was so obviously inaccurate that it was disavowed by the editor of the journal in which it was reprinted (T. P. Jones, 1828, p. 144). Other references bearing on that part of the controversy involving rattlesnake habits will be found in the *Magazine of Natural History*, vol. 6, pp. 464, 466, 551; vol. 7, pp. 67–69, 74, 164–165, 281; vol. 8, pp. 190–192, 540–541, 663–667. Waterton (vol. 6, p. 466; vol. 7, pp. 67, 69, 281) makes much of Audubon's having stated that a rattler was seen to swallow a squirrel tail first; while this is unusual, such an occurrence has been repeatedly noted by competent observers, as mentioned under food habits (chap. 9). Waterton eventually admitted that rattlesnakes climb trees (1835a, p. 663; 1851, p. 203), but still took exception to Audubon's account of how the rattler chased the squirrel up the tree and through the branches until it was caught.

Among Audubon's defenders were Abert (1831, p. 221) and Bachman (1834,

<sup>17</sup> See Swainson's review, *Magazine of Natural History*, vol. 1, p. 48. The mockingbird plate, with the attacking rattlesnake, is plate 21 of the original elephant folio edition of 1827–30; plate 28, vol. 2, of the quarto edition of 1840–44; plate 138 of the New York folio reprint of 1860; and plate 21 of the quarto reprint of 1937. The controversial fangs do not show clearly in the latest reprint.

p. 164). More recently Colles (1908, p. 311)<sup>18</sup> and Herrick (1917, p. 76) have voiced the theory that Audubon had unfortunately confused with his rattlesnake notes some observations he had made of a black snake catching a squirrel. No doubt this was the case. The controversy has also been discussed by Rourke (1936, pp. 170-171, 239-243) and Arthur (1937, p. 216-217). Arthur closes the argument by citing the experience of a friend of his who found a canebrake rattlesnake on the branch of a fig tree 20 feet above ground. But, after all, mere tree-climbing was not the main point of Waterton's criticism; on most of the herpetological points raised in the discussion Audubon was definitely vulnerable. I bring the matter up at this point only because the argument resulted in an extensive airing of opinions on the climbing ability of rattlers, and newspaper accounts (e.g., Dobie in the *Austin American-Statesman*, April 15, 1945) of rattlers found in trees are likely to cite the occurrence as proof that Audubon was right. And so he was—on this point only.

#### CHARACTERISTICS OF TREE-CLIMBING SNAKES

Oliver (1946, p. 295) has pointed out that species of snakes which are persistent tree-climbers usually have these functional modifications: 1) The body and tail are relatively elongated so that the weight may be distributed over a greater length; 2) there is a longitudinal keel or ridge on each side of the belly that enables the snake to utilize minute crevices or irregularities in climbing; 3) the body is laterally compressed so as to afford greater rigidity when spanning gaps between branches. The rattlesnakes have none of these advantageous modifications, but still they are able to climb, after a fashion, by wedging themselves into bark crevices, and by making partial (not full) loops on the upper side of every branch or other protrusion from the trunk of a tree.

A snake progressing out on a horizontal limb, rarely if ever coils around the limb; rather it drapes itself with loops falling below the limb on either side. Stewart (1933, p. 464) showed how snakes (not rattlers) were able by this means to crawl along a horizontal wire.

Although I think it has been amply demonstrated that rattlesnakes do occasionally climb trees, and to considerable heights, they do not do so habitually, and tree-climbing is not a preferred method of securing prey. Certainly Lacépède (1788-89, vol. 2, p. 409; Kerr, 1802, vol. 4, p. 263) was in error when he described the great agility with which the trees were climbed and the celerity with which a rattler could follow prey from branch to branch. Theiss (1925, p. 109) was correct in doubting that a rattler could go straight up a vertical tree, if it was to be inferred that those who told him it could, meant a tree with a smooth trunk, with neither bark crevices nor protrusions. Erwin (1946, p. 28) tells a fantastic story of rattlesnakes that escaped from dogs by ascending trees.

<sup>18</sup> Colles makes the interesting suggestion that viperine snakes do not climb trees because they are prevented from seeing objects overhead by reason of their projecting supraocular scales. But, as has been shown, even sidewinders, whose supraoculars are most exaggerated, occasionally climb, as do some species of *Bothrops* and *Atheris* with projecting supraoculars.

## SWIMMING ABILITY

Although rattlesnakes are not so aquatic as the sea snakes found in the tropical oceans, or even as accustomed to water as are the water snakes (*Natrix*), the garter snakes (*Thamnophis*), or the water moccasin (*Agkistrodon piscivorus*) of our own country, nevertheless they are good swimmers. Some species frequent marshy areas, as does the eastern massasauga (*Sistrurus catenatus catenatus*); one, the Mexican lance-headed rattler (*Crotalus polystictus*), lives—among other places—in the tules of Lake Chapala; and the eastern diamondback (*C. adamanteus*) is sometimes found at sea swimming to and from the keys along the Florida coast. And it is clear, both from published accounts and from the statements of my own correspondents, that all rattlers will take to the water and swim readily enough when their travels in search of food, refuge, or mates require them to cross intervening water. Snakes—rattlesnakes included—are quite buoyant, since the pause in respiration is long and comes after inhalation, instead of expiration as in mammals. Furthermore, the functional lung includes a bladder-like, nonvascular prolongation that increases its air capacity. Thus rattlesnakes float readily, and a sinuous motion of the body and tail propels them at a fair rate of speed.

## HOW THE RATTLES ARE HELD

As early as 1634 the statement was made (W. Wood, p. 48) that if rattlesnakes swim a river they die upon reaching the other shore. This was repeated by S. Clarke (1670, p. 42) and Josselyn (1675, p. 114), but Kalm in 1753 (1752–53, p. 52; 1937 reprint, p. 613) reported that they float like bladders; and Lacépède in 1789 (p. 411; Kerr, 1802, vol. 4, p. 266) wrote that they took to water readily. These later ideas are nearer the truth.

A number of authors have stated that swimming rattlers always swim with their tails elevated to keep their rattles dry (e.g., Rutledge, 1935, p. 423). Dobie (1923, p. 88) reported, as a popular belief, that a rattler never permits its rattles to become wet. The truth of this presumption, now virtually folklore, has been denied by West (1929, p. 35), Hightower (1945, p. 42), and others. Sedlon (1946, p. 96) published a photograph of an eastern diamondback swimming a Florida river; the rattles are not elevated.

My own correspondents have differed on this point. The following state that the rattles are kept above water:

Rattlesnakes often swim in a lake or stream, but they swim with the rattles sticking up out of the water. *J. Lawton Huggins, Game Warden, Mullins, S. C.*



I have seen two rattlesnakes swimming in lakes. They were swimming with head and tail both up out of the water. The tail was held considerably higher than in average snakes and they seemed to swim with the body more than the tail.—*J. A. Hale, District Game Warden, Boligee, Ala.*



I saw a rattler come to a small river on the opposite side from me, and swim across holding its rattles out of the water. *W. A. Spiller, District Warden, Haleyville, Ala.*

I have the skin of a 6-foot rattler that I killed from a little row boat as it was swimming the Halifax River in Florida. It was a hundred yards from land, in choppy water, with head and tail held above the surface, swimming toward a mangrove island. *Josiah Keely, Huntington, N. Y.*



I saw a large rattler swimming a good 300 yards from shore in a reservoir. Its head and tail were above water. *C. G. Holzworth, Kremmling, Colo.*



I have seen rattlesnakes swimming in rivers many times; and, in all cases, their rattles were held out of the water. *J. T. Kenney, U. S. Forest Service, Dardanelle, Calif.*

In these accounts, 5 subspecies of rattlesnakes are mentioned—timber, canebrake, eastern diamondback, prairie, and northern Pacific.

Several others of my correspondents have stated that the snakes keep their rattles dry while swimming, but their accounts were based on hearsay and hence are not repeated here.

The following observers noted instances when the rattles were not protected from wetting:

Rattlesnakes have been seen swimming across rivers in the southern Appalachians. They were not holding the rattles above the water, as I have heard they did. *Herbert P. Rice, U. S. Forest Service, Meadville, Miss.*



I have seen several rattlers swimming across creeks and rivers. Upon reaching the opposite bank they stop and wait for their rattles to dry out. Their rattles become water-logged while they are swimming and they cannot rattle when they reach the shore. They are very dangerous then, as there is no warning rattle to put you on guard. *William Lakanen, Game Warden, Rawlins, Wyo.*



I saw a rattlesnake once in Hobble Creek Canyon near Provo, Utah. It had just come out of a creek, had its rattles full of water, and I nearly stepped on it because it could not be heard, even though it was buzzing vigorously. *R. C. Anderson, U. S. Forest Service, Ogden, Utah.*



On May 1, 1936, while fishing in Little Lake on Kern River, I was sitting on a large rock and noticed something swimming near the center of the lake, about 200 feet from the shore. I watched it come in and discovered it was a 6-rattle Pacific rattlesnake. It was swimming with no apparent effort to keep its rattles dry. I saw another crossing the San Joaquin River, near Mendota. *E. L. Shellenbarger, U. S. Forest Service, Lone Pine, Calif.*

These accounts mention three of the subspecies that have previously been listed as protecting their rattles—canebrake, prairie, and northern Pacific rattlers—and one other, the Great Basin rattlesnake. Therefore the reputed differences in conduct cannot be attributed to a species difference.

Ross Allen, from his long experience with diamondbacks in Florida, had this to say about this apparent conflict of observations:

We have experimented with rattlesnakes swimming and the summary of results is as follows: When a rattlesnake swims in a natural state on open water in a leisurely, unafraid manner, he keeps his rattles up in the air about 70 per cent of the time; but if he is frightened and disturbed, or wants to make more progress swimming, the tail goes down in the water and he makes no attempt to keep the rattles dry.

My own experiments have produced more uniform results, all tending to controvert the dry-rattle story. I experimented with 21 species and subspecies of rattlesnakes by placing them in a fresh-water pond. Those tested included western

diamondbacks (*C. atrox*), Mexican west-coast rattlers (*C. b. basiliscus*), sidewinders (*C. c. cerastes*, *C. c. cercobombus*, and *C. c. laterorepens*), South American rattlers (*C. d. terrificus*), timber rattlesnakes (*C. h. horridus*), Omilteman small-headed rattlers (*C. i. omiltemanus*), mottled rock rattlesnakes (*C. l. lepidus*), southwestern speckled rattlers (*C. m. pyrrhus*), blacktails (*C. m. molossus*), Arizona twin-spotted rattlers (*C. p. pricei*), red diamond rattlers (*C. r. ruber*), Mojave rattlers (*C. s. scutulatus*), tiger rattlers (*C. tigris*), Aruba Island rattlers (*C. unicolor*), prairie rattlers (*C. v. viridis*), southern Pacifics (*C. v. helleri*), Great Basins (*C. v. lutosus*), northern Pacifics (*C. v. oreganus*), and eastern massasaugas (*S. c. catenatus*). In these experiments the snakes were lowered into the water gently so as to frighten them as little as possible. All swam readily, using the same side waves or lateral undulations of the body<sup>10</sup> adopted by other snakes in swimming, including such water-frequenting genera as the water snakes (*Natrix*) and garter snakes (*Thamnophis*).

The rattlers that I tested seemed unafraid of the water, and were so buoyant that their heads and necks could be raised well above the surface—12 inches in large specimens—so that they could look about and get their bearings. They could easily climb a wall 6 or 8 inches high to get out of the pond.

As to trying to keep their rattles dry, the actions of all of these different kinds of rattlesnakes were remarkably uniform; they made no apparent effort to hold their tails above water, even when floating motionless; and as soon as they wished to move, they regularly used their tails for propulsion, with their rattles below the surface. Occasionally when resting or floating, the rattles were held above the surface, but this seemed to be more a repetition of their usual land-crawling posture with the rattles pointed upward than an attempt to keep the rattles dry. Even when resting on lily pads, they seldom avoided trailing the rattles in the water, although they might easily have kept them out.

#### ACTIONS IN THE WATER

Rattlers shed water readily—that is, the skin seems protected from wetting by an oil film, but this does not apply to the rattles. If annoyed, the snakes of my experiments rattled, or tried to, while the tails were immersed, and the rattles became thoroughly wet and at least partly filled with water. If, when rattling, the tip of the rattle was raised above the surface, it was surrounded by concentric rings of vibration wavelets. When a snake was removed from the water, the rattle was first heard faintly, but the sound increased as the water was shaken from the rattles. My experiments lead to the conclusion that rattlesnakes rarely, if ever, make any effort to keep their rattles dry when swimming; their method of using both body and tail for progression precludes their doing so.

Several of the rattlers with which I experimented drank water while floating. Some of my correspondents mention the notable buoyancy of rattlesnakes:

I was fishing in a spring hole, standing in water nearly to the top of my hip boots about 20 feet from shore, when I heard a timber rattlesnake rattle. It came out of the willows and started to swim toward me, and puffed up to half again normal size when it hit the water.

Paul D. Wilcox, State Fish Warden, Wyalusing, Pa.

<sup>10</sup> Cowles (1953, p. 14) reported that sidewinders swim normally in water unless it is quite shallow, in which case they progress by sidewinding.

While trout fishing near Red Bluff some years ago, I saw a northern Pacific rattler swim a stream, in which I was standing. This snake came to the edge, drank and then swam across. It swam with its head high out of the water. *R. M. Williams, Arbuckle, Calif.*

The buoyancy of swimming rattlers has been mentioned by Kalm (1752-53, p. 52), Daudin (1801-4, vol. 5, p. 309), and Tome (1854, 1928 ed., p. 115). Luger (1883, p. 266) said rattlers inflated like an air bubble while crossing a river.

This buoyancy makes it possible for a rattler to strike while floating or swimming in a stream. Schrenkeisen tells of a man who was struck by an eastern diamondback as he waded in water a foot deep.

I have teased rattlesnakes and pushed them into the Snake River with sticks. They swim well. I have rowed alongside of them in a boat, teasing them with an oar, and found they can strike while swimming. *Albert Madarieta, Oakley, Idaho.*



Russell Edgar of Albuquerque, who is on the State Game Commission, told me that on two occasions he has encountered rattlesnakes<sup>20</sup> swimming in Elephant Butte Lake, one about 40 yards and one about 100 yards from land. Mr. Edgar said that upon approach of the boat, the snakes coiled loosely in the water, raised their heads and struck at an oar that was pushed toward them. *A. E. Borell, Regional Biology Division, Albuquerque, N. Mex.*

As has been stated, rattlers swim as do other snakes, with a lateral undulatory motion.

A timber rattler was sighted in the middle of a fish pond, about midway across. The arm of the pond where the snake was crossing was about 150 feet wide. The snake progressed rather slowly, with a wriggling motion, and with its back exposed. *Charles O. Handley, Fish and Wildlife Service, Blacksburg, Va.*



I saw a rattler plunge into a pool 30 feet wide and swim across. It went in with a splash, swam with the head out of water a couple of inches, and had the same motion while swimming as when crawling on land. *Walter F. Emerick, Division of Fish and Game, Palmdale, Calif.*

The following account suggests that rattlers may sometimes depend upon the wind to carry them along:

I have seen rattlesnakes crossing a lake. They coil as if to strike, with head and tail up, filling themselves with air until they look about twice natural size, and then let the wind and the waves take them across. And when I have approached them in a boat, they struck as if they were on the ground. *Leon Stowe, Game Warden, Graford, Tex.*

Several of my correspondents refer to the swiftness of the rivers which rattlers may cross:

Rattlesnakes are good swimmers and readily cross streams if they so desire. I have seen five different ones swim streams that were 6 to 25 feet wide and with a swift current. *M. R. Hickel, Salida, Colo.*



We quite often see rattlers swimming the Big Hole River, a favorite fishing stream some 75 to 100 yards across, and fairly swift. *William T. Sweet, Butte, Mont.*

Rattlesnakes don't drown easily; this endurance would be expected in a cold-blooded animal, with a low metabolism and extra air storage capacity in its single lung:

<sup>20</sup> Probably western diamonds (*C. atrox*).

I have thrown prairie rattlesnakes in the water and they can swim quite well. In fact, we tried to drown one under water for nearly half an hour but it wouldn't drown. *C. H. McDonald, U. S. Forest Service, Stevensville, Mont.*



I found a Pacific rattler trapped in a waterhole in the rocks. I held it under water for 20 minutes trying to drown it, with no success. *R. L. Kloppenburg, U. S. Forest Service, San Luis Obispo, Calif.*

Browning (1860, p. 380) mentions a similar unsuccessful attempt at drowning a rattler.

Several correspondents comment on the fact that rattlers frequent the shores of streams or ponds to drink, particularly in summer, and that occasionally they take to the water to keep cool:

The summer of 1934 was exceedingly warm, with a low relative humidity at the Niobrara Wildlife Refuge, Nebraska. Prairie rattlesnakes were often observed lying in the cool waters of the Niobrara River. The head was invariably on shore and when disturbed, the snakes tried to escape toward shore, in no case retreating into the river. *W. E. Beed, Fish and Wildlife Service, Waupun, Wis.*



I have never seen a rattler in water, except in a slough in August or the latter part of July, when the weather was very hot. The rattles were so wet they couldn't even buzz. *Gustave W. Koski, U. S. Fish and Wildlife Service, Windham, Mont.*

Winfield H. Line told me of having found a speckled rattlesnake (*C. m. pyrrhus*) lying coiled in a small mountain stream that was trickling over, but not completely covering, its coils.

Through Commander G. W. Danforth of Napa, California, I learned that, of 10 northern Pacific rattlesnakes (*C. v. oregonus*) found close to nearby Millikan Lake between April 17 and June 28, 1950, two were swimming in the lake. Another, found on the bank, readily swam across an arm of the lake some 40 feet wide.

Gass (1807, p. 113) mentions a prairie rattler seen swimming in the upper Missouri River near Three Forks. A century and a half later Mosimann and Rabb (1952, p. 26) found another in the same part of Montana swimming in the Marias River. Neill (1948, p. 113) saw canebrakes (*C. h. atricaudatus*) swimming across certain lakes in Georgia in August and September, and always at the same place.

#### REASONS FOR SWIMMING

Several correspondents think rattlers will swim only to escape an enemy, or if forced to by some other threatening situation:

I have seen two Pacific rattlers take to the water to escape, and actually swim across a creek about 60 feet wide. *M. W. Durham, U. S. Forest Service, Pasadena, Calif.*



I can recall seeing only one rattler swimming a river. I believe he had fallen in when trying to get away prior to my seeing him. He got out as soon as possible. *Howard W. Higgins, U. S. Forest Service, Avery, Idaho.*



The only instance I have observed of a rattler swimming was when one was coerced. In that instance it did well and swam the Klamath River to the farther shore. *George S. James, U. S. Forest Service, Yreka, Calif.*

I have never seen a rattlesnake in water unless he was crowded into it. I surprised one along a creek bank and started after him. He went down into the water and swam across. The creek was about 8 feet wide and the water was barely moving. *Eddie Buchta, Fish and Wildlife Service, Moneta, Wyo.*



I have seen rattlers swimming to get away from fire, but have never been able to drive one into the water, although they can swim very well. *Lawrence Kelly, Harper, Oreg.*

Ramsey (1945, p. 39) says that rattlers swam to new refuges when the Conchas Reservoir in New Mexico filled. I had hoped to collect a lot of rattlers on the islands in Lake Mead, formed by Hoover Dam, as the water rose when the dam filled for the first time, but got only a single sidewinder, although I visited a number of islands as they were being inundated. This indicates that the rattlers—Panamint and Mojave rattlers, and sidewinders—must have escaped to the shore by swimming (Klauber, 1939a, p. 81). The swimming proclivities of rattlers, as affecting dispersal and control, are discussed elsewhere (pp. 607, 1026). The snakes are often carried downstream by river floods and usually survive.

#### AQUATIC ACTIVITIES OF PARTICULAR SPECIES

The following notes bear on the aquatic activities of some of the species not previously mentioned as having been seen swimming in the wild:

##### *Western Diamond Rattlesnake (C. atrox)*

I know of cases that prove rattlesnakes do swim streams and lakes. A rancher here, A. N. Lyall, was about half-way across Roosevelt Lake at a point where it is approximately one mile wide, and saw a rattlesnake swimming toward the south shore, and making good time. Another fisherman saw a rattlesnake some distance off shore in the same lake and killed it with an oar. *A. L. Alexander, U. S. Forest Service, Roosevelt, Ariz.*



I once saw a rattlesnake swimming in Roosevelt Reservoir a quarter of a mile from the shore. It seemed to be crossing the reservoir, which was a mile wide. *E. S. Bliss, U. S. Forest Service, Coyote, N. Mex.*

Although there is no final proof that these were western diamonds, this species has been collected on the shore of the lake.

J. Frank Dobie (1945) has reported that rattlers were seen swimming in Aransas Bay, off the coast of Texas, to and from the coastal islands. Without doubt these were western diamonds. Davenport (1943, p. 107) reported western diamonds seen at sea 15 miles off shore.

*Red Diamond Rattlesnake (C. r. ruber).*—This subspecies has been observed swimming in both Sweetwater and Lower Otay reservoirs in San Diego County, California.

On two occasions I have heard of rattlers swimming in the Pacific Ocean, once off the mouth of the Tia Juana River, once off La Jolla. Whether they were red diamond rattlers or southern Pacifics could not be determined; both species are not infrequently found on the sand of the shore above the high-tide line.

##### *Panamint Rattlesnake (C. m. stephensi)*

In April, 1943, I saw a Panamint rattlesnake swimming across a small cove in the Colorado River near Eldorado Canyon. He had almost reached the bank when I saw him and I could

see no reason why he had taken to the water. *Gordon C. Baldwin, Boulder Dam National Recreational Area, Boulder City, Nev.*

*Eastern Massasauga (S. c. catenatus)*

The only rattlesnake I ever saw in the water was a *Sistrurus catenatus* in Jackson County, Michigan. It was seen swimming in a little creek that meandered through a marsh in which the water circulated about tussocks of marsh grass. As it was swimming, it stuck its head out and looked around almost within my reach. *Carl L. Hubbs, Scripps Institution of Oceanography, La Jolla, Calif.*

Conant (1938, p. 115) also states that this subspecies enters water occasionally. Fox (1948, p. 63) reported one seen swimming in Georgian Bay, Ontario, about a mile and a half from the shore.

*Western Pigmy Rattlesnake (S. m. streckeri).*—R. M. Perkins writes that a friend found a specimen of *streckeri* swimming the James River, bordering Stone County, Missouri. It was preserved for identification.

*Eastern Diamondback (C. adamanteus).*—Undoubtedly the champion salt-water swimmer among the rattlesnakes, at least of those found in the United States, is the eastern diamondback (*C. adamanteus*) of Florida and the adjacent states. Here are some observations on their seagoing propensities:

Two friends of mine killed a diamondback rattler in the Gulf of Mexico, 2 miles from land. This snake evidently was going from an island to the mainland. Another was killed swimming in Lake Marianna, near Auburndale, Florida. *Joseph T. McCullough, U. S. Forest Service, Brooklyn, Miss.*



For years I had heard, from the fisherman-farmers of Sanibel Island, Lee County, Florida, that the only rattlesnakes on the island were those that had swum over from the mainland, which they soon found and killed. Sanibel is in the Gulf of Mexico, off the mouth of the Caloosahatchee River. Early in the spring of 1935, we were dredging for bottom fauna from a guide boat in the northern part of San Carlos Bay, about 200 yards off the southern end of Pine Island. We saw a snake swimming from Pine Island, apparently toward Sanibel. We moved up to it and picked it up in a dip-net. It was a rattlesnake not more than 30 inches long. We turned it loose, and the snake continued on in the same southwesterly direction. We watched it for quite a time. Sanibel is about a mile from Pine Island, and the last we saw of the snake it was fully a third of the way across. The current was not strong, and there was little wind. I do not remember which way the tide was setting at the time, but whether in or out, the rattlesnake was swimming cross current. *Margaret Storey, Stanford University, Calif.*

Ross Allen of Silver Springs, Florida, reports:

The Florida diamondbacks are often found swimming wide waterways, and, on one occasion, one was found floating in the Gulf of Mexico, 22 miles from land, apparently having floated out with the tide at night. Rattlesnakes do not hesitate to swim across salt water, even great distances from island to mainland.

Rutledge (1935, p. 523) reports having seen a diamondback off the Georgia coast, a mile and a half from shore, between a barrier island and the mainland. Carr (1940, p. 95) says they have been taken in mackerel nets several miles out in the Gulf of Mexico. S. C. Clarke (1881, p. 406) saw a 5-foot diamondback swimming a salt-water sound 1 to 2 miles wide. As his boat approached, the snake swam toward it. Loennberg (1894, p. 335) says they frequently swim from key to key.

*Northern Pacific Rattlesnake* (*C. v. oreganus*).—Some species of rattlers that swim lakes and rivers also may cover considerable distances, as in the case of this northern Pacific rattler:

Last April, at Lake Millerton, I observed a snake swimming in the water and thought it a gopher snake. Upon going to the point where it landed on shore, I saw it was a 4-foot rattler. It swam with ease and had evidently come from the opposite shore, a distance of 300 or 400 yards. *Paul J. Kehrer, Warden, Fresno, Calif.*

*Mexican Lance-Headed Rattlesnake* (*C. polystictus*).—Little is known about this rattlesnake; it may be semiaquatic, judged by the following report from Paul D. R. Ruthling of Santa Fe, New Mexico:

The *polystictus* which I collected at the mouth of Río Lerma, Lake Chapala, Jalisco, Mexico, were extremely abundant among the rushes, of which there were two kinds, the flat and the round. In almost every clump of the round rushes, these snakes were found. This was in flooded swamp land, and the snakes were above the water. They would usually dive into the water when approached, but sometimes they would allow the canoe to come within arm's reach. All specimens were far from land. At the time, I did not realize the value of the find, and thinking them a very common species, did not collect as many as I could have secured.

*South American Rattlesnake* (*C. d. terrificus*).—Clark (1953, p. 30) saw a rattlesnake swimming in one of the remote tributaries (the Ucayali) of the upper Amazon River in Peru. He believes the South American rattler to be semiaquatic (p. 340), which is certainly not true of *terrificus* over most of its range, for it is most prevalent in arid places. Of course there might be an unknown species or subspecies of distinctive habits in the rarely explored sources of the Ucayali River, but if there were aquatic rattlers in South America, they might well be expected along the lower Amazon. No doubt *terrificus* can swim well enough when the necessity arises at a time of flood, for this is true of all rattlesnakes, but this does not indicate that it is aquatic.

#### TALES OF SWIMMING RATTLESNAKES

Among the decidedly doubtful stories of the prevalence of rattlers in water are the following:

Catlin (1868, p. 12) says that rattlers were seen in Pennsylvania to cross rivers and lakes by the hundreds and thousands on the way to their dens. Anon. (1873, p. 125) tells of a man rowing out in Lake George, New York, and killing 29 rattlers. Lugger (1883, p. 266) expresses the erroneous belief that rattlers take to water only when chasing prey at night. Evers (1951, p. 110) believed that rattlers would not cross running water unless a bridge was provided.

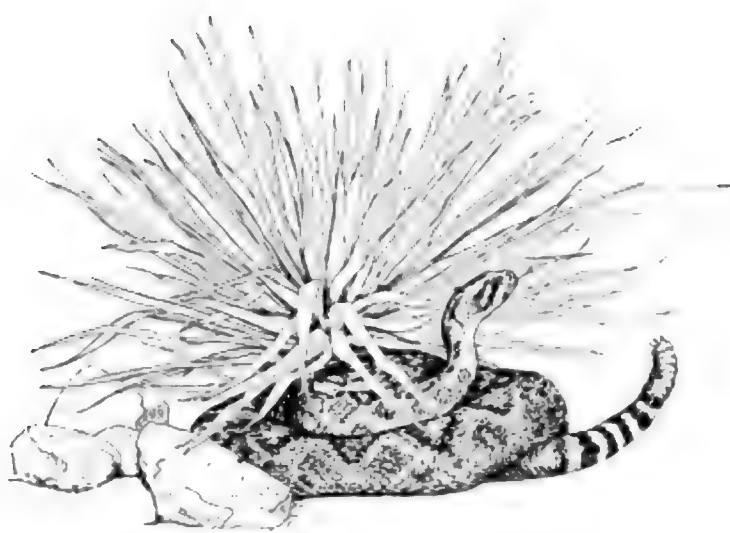
Another story requiring confirmation is that of West (1929, p. 35), who reports that a timber rattler, swimming in a river, paused and coiled when he whistled at it at a distance of 30 feet. Swimming moccasins will stop at a whistle nine times out of ten, according to West.

Carmer (1936, p. 321) found a backwoodsman in upper New York who pleasantly combined two myths when he told of a mother rattler which protectively swallowed her young and then transported them across Lake George with her tail in the air, rattling like an outboard motor.

## DANGER FROM SWIMMING RATTLESNAKES

Although there can be no doubt as to the swimming ability of rattlesnakes, they can be easily avoided by anyone in a boat having a weapon or means of propulsion. Lacépède (1788–89, vol. 2, p. 415; Kerr, 1802, vol. 4, p. 272; Daudin, 1801–4, vol. 5, p. 309) was greatly exaggerating when he stated that they swim with the speed of an arrow, and endanger people in small boats. Conceivably a rattler, tired from swimming, might try to climb into a boat, but it would be easy to thrust it off with an oar or stick. Fishermen on the freshwater lakes of San Diego County are sometimes badly frightened by southern Pacific and red diamond rattlers that swim near the boats. Although the most sinister motives are attributed to these naval attacks, we may be sure that a rattler, if it approaches a boat, is only seeking a temporary resting place.

Although a rattlesnake could bite under water, a person must be careless indeed, who would get near enough to a swimming rattler to be within its striking range and then proceed to annoy it into biting. Payne (1872, p. 223) and Ellzey (1884, p. 253) have reported fatal water-moccasin bites in water, but these snakes are far more prevalent and at home in water than rattlesnakes.



## 8. Populations and Ecology

### INTRODUCTION

Who, in wandering about the hills in search of rattlesnakes, has not wished for a special Geiger counter responsive to some unknown *Crotalus* emanation, whereby he might locate every rattler in the area, hidden though it might be, in the weeds, under a stone, or down some mammal hole? For the secretiveness of these snakes keeps them in hiding much of the time, and even when in the open their pro-cryptic color patterns make them difficult to see. Altogether, the most experienced hunter, except at denning time, or in a sandy desert where they may be tracked, will never find more than a small fraction of the rattlers in his area.

Necessarily our knowledge of rattlesnake population densities is quite inadequate, for the technique productive of the most accurate data, that of tagging, releasing, and recapturing as many individuals as may be found, requires a long-range program, and has only begun to be applied. Also, with venomous snakes such as rattlers, this experiment should never be countenanced except in remote areas where there will be no danger to persons or livestock from the snakes released. But at least, from the data at hand, we may learn something as to the proportion of snake populations that rattlesnakes comprise, and whether two or more species may commonly occupy the same ecological niche. For much is being learned of the character of the surroundings frequented by the different kinds of rattlers.

### THE IMPORTANCE OF ECOLOGICAL FACTORS

In a study of rattlesnake populations, it will be desirable, first, to discuss their ecology, the habitats wherein they are found, and the conditions that govern their lives and limit their spread. A preliminary survey of rattlesnake ranges makes it evident immediately that the various species and subspecies are subject to quite different ecological requirements and limitations.

Rattlesnakes are restricted to the New World; they have a vast range in the Americas from Lat. 51° N. to Lat. 35° S. In this area they occupy many different types of terrain—deserts and jungles, valleys and mountains, sand dunes and forests, mainland and islands. But no single species includes all of these habitats

in its range; this wide variation appertains only to the rattlesnakes as a group. Each species has requirements of its own, sometimes quite restrictive, in others more inclusive. To be definite as to these requirements it is necessary to discuss habitats by species, rather than in a group generalization, and this I shall do, although some repetition is thereby involved.

If there is one generalization which may safely be expressed it is that, by and large, rattlesnakes live in dry areas. Although there are specific exceptions, to be mentioned in due course, most species and probably more individuals, are to be found in arid places. Deserts, grassy plains, and brushy or rocky hills appear to be more suitable for rattlesnakes than areas clothed with trees. It is for this reason, as well as because of varied topography, that Arizona contains more species and subspecies than any other state, and that many species are restricted to the southwestern United States and northwestern Mexico.

The primary factors affecting distribution are food supply, climate, and refuges. Rattlesnakes live to a large extent on small mammals, with lizards as the second most important component of diet—indeed, the most important in the case of some species and the juveniles of others. Ranges and population densities are first of all dependent on food availability. With respect to temperature, it should be pointed out that rattlers, like other reptiles, having no metabolic temperature-control similar to that which renders birds and mammals so independent of exterior temperatures, must confine their activities to times and places where air and ground temperatures, and radiation, are such as to produce body temperatures within a relatively narrow range—say 65° to 95° F. (18.3° to 35° C.). Temperatures too low are more serious than those too high; to avoid high temperatures the snakes can and do take refuge in ground holes, rock crevices, or the dense shade of brush, restricting their pursuit of prey to the night hours. But in a suboptimum temperature there is no escape from an inevitable lethargy and even immobility; digestion, muscular activity, and the reproductive processes slow down or cease. Against these effects, a winter den is only a place where immobility can be made safe but may not be prevented. Thus rattlers cannot live in places where the season of adequate temperatures is too short for fat accumulation, growth, and reproduction.

Changing climates of the distant past have produced the discontinuities in the ranges of the rattlesnakes as we see them today, such as that of the Arizona black rattlesnake (*C. v. cerberus*) in Arizona, where it is now restricted to the timbered areas of the central section and a few mountain ranges of the south, this population having become separated by intervening deserts from its close relative, the southern Pacific rattler (*C. v. helleri*) along the southern California coast. Other examples are the montane-island populations of the Arizona twin-spotted rattler (*C. p. pricei*), the banded rock rattler (*C. l. klauberi*), and the Arizona ridge-nosed rattler (*C. w. willardi*) in the mountains of southeastern Arizona.

Ecological changes produced by man, particularly in agriculture, generally result in conditions less favorable to rattlers than the original primitive conditions to which, through the ages, they had become inured, so that land clearance and cultivation usually decrease the rattler population, even though there may be an increase in the food supply. And there are not only the changes in surroundings and the destruction of refuges to be counterbalanced, but the ever-

present enmity of man and his domestic animals. For example, the massasauga, once common on the prairies of the upper Mississippi Valley states, has now retreated into the marshes or wastelands; the sidewinder has disappeared from the irrigated sections of the Imperial and Coachella valleys in southern California, although still common in the adjacent desert; and the prairie rattlesnake has been driven out of the farm lands of Kansas and Nebraska.

Although human occupation, with agricultural and industrial developments, has now eradicated rattlers from many extensive areas they once frequented, it is of interest to note that in primitive times few sections of the United States were not tenanted by at least one species of rattlesnake. Aside from the mountain peaks—above 11,000 feet in California and 9,000 feet in most other areas—the only unoccupied places were northern and eastern Maine, northeastern Wisconsin, upper Michigan, northern Minnesota, northeastern North Dakota, northwestern coastal Oregon, and western Washington. It is probable that in pre-Columbian days at least some part of every state was inhabited by rattlesnakes. Some of the extirpations occurred at a comparatively early date. For example, Kalm (1752–53, p. 132; 1758, p. 286) commented that rattlers were even then rarely seen about settled communities. Dwight (1823, p. 29) said that people in New England and New York no longer had cause to feel any anxiety about them.

Rattlesnakes have been quite successful in maintaining themselves on some islands, particularly off the coasts of California and Baja California. Although some of these colonies may have resulted from implantations subsequent to insular separation, it is probable that many of them predated such separation. These island populations have gradually diverged in character from their mainland congeners until several have justified specific or subspecific recognition. Others show recognizable differences which do not yet warrant nomenclatorial segregation. The same is true of some of the montane-island forms.

## RANGES

### RANGE LIMITS

One should never presume, from a range map, that the animal whose range it purports to show is to be found everywhere within the cross-hatched area. Even a map with dots to indicate the localities where the creature has been observed, fails to reveal how sporadic and interrupted such ranges usually are. For there is a great ecological variation and consequent habitability or inhabitability in almost every area, quite beyond the capacity of any map to disclose, unless a prohibitively large scale be used. Even in an area of once uniform characteristics, there are changes wrought by human activities—grazing, agriculture, irrigation, fires, and other conditions that produce local diversity.

So the experienced collector views a range map only as the outline of an area in some ecological niches of which a certain animal, such as a kind of rattlesnake, may be or was once found, not as a district in every part of which it will be found. Look, for example, at the map of such an expanse as the Mojave Desert. Here we have a vast plain, up through which protrude numberless scattered mountain peaks and chains. Any range map would show the sidewinder, the Mojave rattler,

and the southwestern speckled rattler as occupying this territory, but it would fail to disclose the fact that the first two live almost entirely on the flats, and the last near or in the mountains. Similarly, the little Arizona twin-spotted rattlesnake, the banded rock rattlesnake, and the ridge-nosed rattler, though found over a considerable territory in southeastern Arizona, actually occupy quite restricted sections of a few rather short mountain ranges. It would be almost as astonishing to find one of these rattlers on the plains between the ranges as to find it in South Dakota.

In addition to these broader habitat selections, there are others more local in nature, for some species of rattlers prefer brush, whereas others in the same district may be largely restricted to rocks or to sandy washes. These preferences are often difficult to determine with accuracy except by continuous local observation, and even then an occasional stray will complicate the record. When these local preferences are taken into consideration, we find that there may be less competition or overlapping between rattlers than might be presumed from the maps. Despite the fact that some 17 species and subspecies of rattlesnakes are found in Arizona, I know of no place where more than 6 occupy the same ecological niche in any area.

The reasons for range limits may or may not be apparent. Limitations premised on food supply or cover are the easiest to explain. Enemies and competitors may be important factors. Some limits are explicable on the basis of ecological differences, although we can seldom go behind these differences and explain just why the rattler in question cannot survive in the different situation beyond its range. For example, the sidewinder is essentially a desert snake, and we may assume that its particular bodily form, method of locomotion, and the other characteristics that render it efficient under desert conditions, prevent it from extending its range into nondesert territories. Whether this is because it suffers in competition with less highly specialized forms or of something inherent in its reaction to temperature and humidity is not known. But at least we can say that it is a desert snake and does not live in nondesert areas, however lacking in basic reasons such a statement may be.

But other range terminations or gaps that we observe in rattlesnake ranges are less easily explained. Why is not the Mojave rattlesnake found in the Colorado Desert, an area that seems so similar to many territories in which it thrives? Why has not the western diamond rattler invaded the desert foothills of the San Jacinto Mountains of California, which resemble many of its Arizona habitats and which are only a few miles from sand dunes where it is plentiful? These range-limitation problems are seldom to be explained upon the supposition that the species in question has not had time to expand its range into the unoccupied territory. There are too many indications of an occasional entry with failure to become established. Usually range limits are basically a question of adaptability; no doubt some particular, but possibly obscure, ecological condition is crucial.

One interesting effect of adaptability is that two or three species of rattlesnakes that seem to thrive equally well in a certain area—for example *helleri*, *ruber*, and *pyrrhus* in the western foothills of San Diego County, California—may have quite different range limits elsewhere; each thrives in some territories which the others find inhospitable; each must have its own crucial limitation factor.

Although there is no question that some species of rattlers are more adaptable

than others, curiously enough there seem to be instances wherein a single subspecies is more adaptable in one part of its range than another. This is true, for example, of the Mojave rattlesnake in Los Angeles County, California, as compared with the same subspecies in Yavapai County, Arizona; the latter seems able to withstand more variable conditions—at least it has invaded rocky foothills and even mountains in Arizona, whereas terrain of similar character acts as a barrier in California.

One of the requirements of rattlesnakes for the occupation of a territory is adequate refuges from adverse weather and from enemies. Thus, in northern climates there must be suitable dens for hibernation, so that freezing and exposure to enemies while the snakes are helplessly immobilized may be avoided. In all areas where the diurnal temperature exceeds that which the snakes can withstand, and this is lower than most people presume, there must be refuges against the heat, and particularly the direct rays of the sun.<sup>1</sup> C. H. Pope (1946, p. 10) points out that a forest or other overhead cover permits a snake to move at will from sun to shade, thus affording, within limits, an efficient means of temperature control. Finally, there must be available refuges from enemies, such as hawks and hogs. Rattlesnakes are usually timid and have a habit of concealment, and, unless actively engaged in the pursuit of food or mates, are likely to spend most of their existence in secluded retreats.

Some range limits are a matter of present accessibility. There are, for example, a number of mountain ranges in Arizona, where some of the mountain species not present would no doubt thrive, but these wooded heights are now inaccessible because of the intervening arid plains that isolate them from the mountains where the montane species do occur. Whether they ever tenanted these unused mountains at a time when the climatic conditions permitted them to reach the peaks they now occupy, and, if so, why they failed to persist on some peaks, is not known.

Where range limits involve rather steep ecological gradients, it is, of course, fairly easy to fix them, though, when one is actually on the ground, it is often difficult to see why the next mile would not have been equally habitable. But sometimes the limit seems to be quite inexplicable; here the species is to be found—over there in what seems to be the same kind of surroundings it is absent. We can only guess that there is effective some deterring feature of climate, food, or shelter, whose presence or effect is not apparent.

Some limits are really nonexistent—they are nomenclatorial only. Thus, for purposes of definition and description, we may divide a species into two subspecies and fix a range limit along the center of the intergradation strip between them. But actually, as far as the species is concerned, there is no boundary here. Sometimes the fact that intergradation between subspecies is normal is not understood; it has been confused with hybridization between species (e.g., Noble, 1954, p. 42).

Taken as a single group comprising two genera, the rattlesnakes are plastic and polymorphic; they have become adapted to a variety of environmental con-

<sup>1</sup> Although desert rattlesnakes seek ground holes at times of extreme temperatures, they probably come out at night (toward morning in summer) whenever the need for food requires. There is no indication of true estivation.

ditions. The division of species into subspecies is so subjective an art that it is hardly feasible to evaluate species plasticity on a basis of the number of subspecies into which a species has been divided. But it is clear that there is some correlation between plasticity, as evidenced by intraspecific character variation, and ecological range, meaning by the latter, not territorial range so much as the diversity of the ecological conditions accepted. The outstanding example of plasticity among the rattlers is the wide-ranging western rattlesnake (*C. viridis*) and its subspecies; whereas the sidewinder (*C. cerastes*) is an example of a snake having great uniformity, in both its characteristics and the terrain wherein it lives.

#### ALTITUDINAL RANGE

In this separate section on the altitudes attained by rattlesnakes, I shall mention only the altitudes achieved by whatever subspecies reaches the highest points, first in the Appalachians, then from the Rockies to the Pacific, and finally in Mexico above 11,000 feet. The purpose of this special treatment of altitudes is to give sportsmen and fishermen (who are seldom interested in species differences) some knowledge of the heights above which they need no longer be on the lookout for rattlers of any kind. This separate discussion will also serve to emphasize the fact that, while not common at high altitudes, rattlesnakes do reach heights above those where they are popularly presumed to exist. The only safe general rule is to be on the lookout for rattlers in the warm season on any mountain in the United States up to 10,000 feet, except in California where the range is extended to 11,000 feet. In Mexico, one small subspecies attains an elevation of at least 14,500 feet. As to the heights reached by other kinds of rattlesnakes that do not hold the altitude records in these three sections of North America, their altitudinal ranges will be mentioned in connection with descriptions of other phases of the habitats in which they occur.

The altitude attained by rattlesnakes is of considerable interest to sportsmen and campers, for they feel reassured when they are at an elevation at which they no longer need be on the watch for rattlers. Wyman (1892, p. 588) said he always pitched his camps above the snake line, if possible. In many western mountain areas, rattlesnakes occur higher than most people assume to be the case. The heights reached are dependent on the rattlesnake species that inhabit the area, and the montane climates. Species reaching the maximum altitudes are generally those that have wide latitudinal ranges; also they are the ones exhibiting adaptability with respect to local habitat conditions, including an ability to survive in rocky areas. The most notable of these species are the timber rattlesnake (*Crotalus horridus horridus*) in the Appalachians; the western rattlesnakes (*Crotalus viridis* and its subspecies) in the Rockies, Great Basin, and Sierra Nevada; and the Mexican dusky rattlesnake (*Crotalus triseriatus*) in Mexico.

As one proceeds north, the maximum elevations reached by rattlers decline, just as the timber line is lower, and for the same reasons. The local conditions of winds and exposures that limit vegetation will also prevent any rattler tenancy of high points. These affect the food supply, comprising small mammals and lizards, and the growing season, which must be long enough for the snakes to reproduce, although, for this, two summers may be required. It should be remembered that snake activity and metabolism are far more affected by external tem-

peratures than are those of warm-blooded animals such as birds and mammals, with their self-regulating temperature mechanisms.

Such data as I have been able to accumulate from my own correspondents or from published statements regarding the three record-holding species of rattlers are as follows:

*Timber Rattlesnake* (*C. h. horridus*).—Let us first consider the Appalachian Mountains. At the northern end, in the New England states and New York, it is doubtful that rattlesnakes reach the highest peaks; for although the snakes have now been limited by the inroads of agriculture and industry to primitive and rocky areas, and the highest points would furnish refuges of this kind, these are climatically too inhospitable. But in the southern Appalachians the conditions are more favorable, and it is probable that timber rattlers are found close to, if not at, the very highest points. (Mt. Mitchell, North Carolina, elevation 6,684 feet, is the highest point east of the Mississippi River.) My correspondents in this area have furnished the following high records:

Last month, while marking timber at an elevation of 4,300 feet, I encountered a rattlesnake in blackberry briars. *C. R. Carr, U. S. Forest Service, Richwood, W. Va.*



I have killed timber rattlers at all altitudes up to 4,000 feet on Beaver Lick and Back Allegheny Mountains. Beaver Lick tower, where I have been a guard in the fire season, is built on a cliff of quartzite rock, 3,662 feet in altitude. It was once a snake den. *J. W. Crigger, U. S. Forest Service, Huntersville, W. Va.*



About the highest elevations we have in this region are 6,000 feet. We find rattlers right on the highest tops. However, they are never as plentiful as on some of the lower slopes. *John H. Stanley, U. S. Forest Service, Andrews, N. C.*



The highest point in the Nantahala Forest is Wayah Bald, altitude 5,316 feet. There is a lookout on the peak and a number of rattlers have been killed under the tower. *E. A. Schilling, U. S. Forest Service, Franklin, N. C.*



In this section I have seen rattlers rather thick on the higher slopes, very close to the top of a 5,000 foot mountain. *Bryce Ledford, U. S. Forest Service, Tellico Plains, Tenn.*



This is to confirm the report previously given you of a rattlesnake killed on Inadu Knob on August 16, 1932. It was within 100 feet (surface measurement) of the summit, which is 5,941 feet in elevation. This is, by far, the highest elevation at which I have seen a rattlesnake or other poisonous snake in the Great Smokies. *Arthur Stupka, Great Smoky Mountains National Park, Gatlinburg, Tenn.*

I have also had reports of rattlers near the peaks of Spruce Mountain (4,860 feet), Pocahontas County, West Virginia; and on Elliott Knob (4,473 feet), and the Apple Orchard and Warm Springs mountains (at about 4,200 feet), Virginia. As to published records, King (1939, p. 578) mentions a rattler taken in the Great Smoky Park at an altitude of 5,500 feet. He says they are uncommon above 5,000 feet. The conclusion appears justified that in the southern Appalachians the timber rattlesnake certainly occurs up to 6,000 feet, and may actually reach the highest peaks.

The subspecies *C. h. atricaudatus*, the canebrake rattlesnake, is essentially a lowland form, and does not attain the altitudes reached by its close relative *C. h. horridus*, the timber rattler

*Western Rattlesnake (C. viridis).*—From the Rocky Mountains to the Pacific Coast, the altitude records in every state are held by some subspecies of the western rattlesnake (*C. viridis*), an adaptable and wide-ranging reptile. Some of these records, segregated by subspecies and by states, are as follows:

*Prairie Rattlesnake (C. v. viridis)*

Rattlesnakes can be found over the entire county up to elevations of 7,000 feet. *T. A. Clapp, U. S. Forest Service, Warren, Mont.*



Rarely are rattlers found above altitudes of 6,500 feet. *A. L. Olson, U. S. Forest Service, Gardiner, Mont.*



The country here is very rough and rugged. I have killed rattlesnakes at 8,400 feet elevation. *John W. Warren, U. S. Forest Service, Hamilton, Mont.*



I have never seen a rattler above 9,500 feet. *Ellen Johnston, U. S. Fish and Wildlife Service, Shelby, Mont.*



Throughout the east slopes of the mountains in central Wyoming, the rattlesnakes go up only to about 7,200 feet. On the west slopes they probably go 500 feet higher, due to the warmer exposure. *Bly Dickson, U. S. Forest Service, Dayton, Wyo.*



I do not think that I have ever seen a rattlesnake here in Wyoming above 8,500 feet. It seems to be too cool at night for them here when they get too high. *Eddie Buchta, U. S. Fish and Wildlife Service, Moneta, Wyo.*



The highest elevation at which I have seen rattlers is on Battle Mountain, about eighty miles south of here, which has an elevation of 9,105 feet. There is an exceptionally large number of rattlers on this mountain, and they have dens there. *William Lakanen, Game Warden, Rawlins, Wyo.*

Another Wyoming high point mentioned by a correspondent is North Fork of Paintrock Creek at 8,200 feet, Bighorn Mountains, Bighorn County. The *Denver Post* of July 14, 1949, said the legend that rattlers could not exist in high country had been rudely shattered the week before, when a sheepherder on Pole Mountain, Wyoming, above 8,000 feet, had been bitten by a rattler.

It has been my observation that rattlesnakes range throughout the suitable areas of this district of the Roosevelt National Forest, up to an altitude of about 7,000 feet. The localities are influenced by habitat requirements, for they prefer rocky, warm, sunny exposures. *H. A. Payson, U. S. Forest Service, Estes Park, Colo.*



Rattlesnakes are seldom seen above 7,500 feet in elevation in this country, except that occasionally they may be found on dry, rocky, south and east slopes up to 8,000 feet. *E. S. Keithley, Colorado Springs, Colo.*



Rattlers have been found at elevation 8,620 in the Trail Junction Picnic Area northwest of Colorado Springs. *William F. Cochran, U. S. Forest Service, Colorado Springs, Colo.*

On the eastern slope, near La Veta, Colorado, I killed a big rattler at an elevation of about 7,100 feet. They are found frequently on the eastern slope at elevations of from 4,000 to 6,500 feet, in the drier localities. They appear to prefer the drier, rocky hillsides of the plains country and up into the oak-brush type. *Ralph C. Bryant, U. S. Forest Service, Ouray, Colo.*



A sheepman has a spring and watering trough at what is estimated to be between 500 and 600 feet below Mogote Peak (elevation 9,820 feet). Several rattlers were found in the vicinity of the trough, which would make the elevation of the snakes 9,220 to 9,320 feet. Two rattlers were killed and several others seen. *M. A. Shoeneman, U. S. Forest Service, Antonito, Colo.*



The highest record of which I have ever heard is on Fawn Creek, where several rattlers have been killed at an elevation of 8,500 to 8,800 feet; seemingly, an isolated den on a rocky south slope.<sup>3</sup> *Benjamin M. Whitehill, U. S. Forest Service, Buford, Colo.*

A. F. Hoffman, of the U. S. Forest Service, advised me that rattlers had been seen at 9,400 feet one mile south of Rock Creek Park, and at 9,500 feet at Gate Creek Park, Rio Grande County, Colorado. In the southwestern corner of the state they have been noted as high as Park Point, 8,575 feet, Mesa Verde National Park.

Rattlesnakes are fairly common in this vicinity and on the Santa Fe National Forest, usually up to elevations of 6,000 feet; rather infrequently up to 7,000 feet; and in at least one or two cases that I know of, have been found as high as 9,000 feet. One such locality was near the northwest corner of the San Diego grant, Sandoval County. *Perl Charles, U. S. Forest Service, Santa Fe, N. Mex.*



In the Manzano Mountains, Torrance County, I have seen rattlers at altitudes up to 10,000 feet. *A. F. Rea, Monticello, N. Mex.*

Another high record from New Mexico is near the top of Barrillis Peak, San Miguel County, at 9,000 feet. Barker (1946, p. 73) reported rattlers at 9,000 and 10,000 feet in northwest Colfax County and northeast Rio Arriba County, New Mexico.

*Great Basin Rattlesnake* (*C. v. lutosus*).—From the Rockies to the Sierra much of the area between the Grand Canyon and central Idaho comprises the range of the Great Basin rattler. In this desert-mountain territory this snake ranges from the flats far up into the mountains.

The highest I have seen a rattler, or heard of one, was at 7,000 feet. I know of several dens at an elevation of about 5,700 feet. The highest dens are mostly on the south slope of a hill, where dirt has covered loose rocks, leaving a small entrance. I helped dig out 50 rattlers at one time. *Floyd C. Black, U. S. Fish and Wildlife Service, Challis, Idaho.*



Elevation is not the controlling factor of rattlesnake habitations, although it may have something to do with it. There are no rattlesnakes around Meyer's Cove at an elevation of 5,100 feet, while there are many of them in other areas at elevations above 6,500 feet. *Lewis B. Koch, U. S. Forest Service, Challis, Idaho.*



The highest elevation at which rattlers are found is about 8,000 feet. This is on Crouse Point of the Challis National Forest, Challis, Idaho. *Ernest H. Taylor, U. S. Forest Service, Victor, Idaho.*

<sup>3</sup> These might be the midget faded rattlesnake (*C. v. decolor*).

In the vicinity of Ogden and Logan, where rattlesnakes are known to be abundant, I have seen them up to 9,000 feet in elevation, in fact, at 9,600 feet. One was within 100 yards of the top of Ogden Peak, on a hot rock. *R. C. Anderson, U. S. Forest Service, Ogden, Utah.*



I recall seeing rattlesnakes at elevations of between 4,000 feet and 8,500 feet. They seem to prefer dry, rocky ridges, although I have seen a few along streams running through rocky canyons. In 1937 I killed a number of them on a ridge at 8,500 feet elevation. The slope was to the west and the area was extremely rocky. The number of snakes in the area indicated that they probably denned there. *Thomas H. Sevy, U. S. Forest Service, Randolph, Utah.*



I have never found a rattlesnake at a higher elevation than 7,800 feet, in this section. Possibly they may be found at higher elevations in rocks and ledges. *J. W. Humphrey, U. S. Forest Service, Ephraim, Utah.*



During the summer of 1929, while making a range inspection, I met two sheepherders at an elevation of 10,050 feet. They told me they had just killed seven rattlesnakes under one large rock by moving the rock and shooting the snakes as they moved about. I questioned this, because of the elevation, but we visited the place and found the report to be true. There were three large adult snakes and four half-grown. *Milo T. Dyches, U. S. Forest Service, Monroe, Utah.*



I have seen rattlesnakes at 9,500 feet elevation in a dry, sage-brush type of country. Maurice Cape of Zion National Park reports seeing one at about that elevation in a timber-type country. *H. Bryson Cook, U. S. Forest Service, Panguitch, Utah.*

Other high Utah records for this subspecies are 8,900 feet in Bryce Canyon National Park (W. W. Tanner, 1940, p. 145), and Big Table, 9 miles east of Alunite, Piute County, at 9,500 feet.

I have never seen rattlers in this state higher than about 7,000 feet. *F. R. Allen, U. S. Forest Service, Wellington, Nev.*



Rattlesnakes seem to prefer hot, rocky or sandy country, and I have seen them in heavy stands of sagebrush. I have found them from the valley bottoms at about 5,000 feet elevation up to over 9,000 feet. I have seen them at elevations of between 9,000 and 9,500 feet, on Savory Peak in the Monitor Range, and Ardivay Peak in the Toyabe Range. *B. K. Crane, U. S. Forest Service, Austin, Nev.*

Other high records in Nevada are Grey's Lake, Elko County, at 8,500 feet; and Allison Peak, Eureka County, at 9,000 feet.

In California I have no records of this subspecies above 8,200 feet (near Mono Lake); this record is considerably exceeded in that state by the northern Pacific rattler. In southeastern Oregon the Great Basin rattler no doubt reaches 6,000 feet or higher, but I have no records above Rockville (3,900).

*Northern Pacific Rattlesnake (C. v. oreganus).*—There seems no question that this snake reaches higher altitudes than any other in the United States, for in the southern Sierra Nevada of California it attains altitudes of somewhat over 11,000 feet. Farther north the more rigorous climate restricts it to lower elevations. The highest Oregon records that I have are Soda Spring (5,700 feet), Jackson County, and Tamarack Mountain (6,900 feet), Grant County. In Washington the maximum records available to me are Icicle Ridge (6,000 feet), Chelan County, and McGregor Mountain (5,800 feet), Okanogan County. From British Columbia I

have heard of none higher than one from Merritt, 2,025 feet. Thus we note a progressive decline in altitude as we proceed northward from the mountains of California.

However, eastward in northern Idaho, a somewhat drier area, where the northern Pacific rattlesnake approaches intergradation with the prairie rattler, somewhat higher altitudes are again reached.

I spent 20 years in the Magruder District, which includes a part of the Salmon River slopes, between Horse and Sabe creeks, and the headwaters of the Selway River. The Salmon River slopes were infested with rattlesnakes, from the river, at approximately 2,000 feet, to elevations up to 8,400 feet. Rattlers were killed almost every year underneath the lookout tower on Square Top Mountain. *F. C. Fitzgerald, U. S. Forest Service, Lincoln, Mont.*

The following data, about the mountain areas of California, have been made available through the courtesy of my correspondents. It will be noted that rattlers are not at all unusual between 9,000 and 10,000 feet, and that the record is about 11,000, the highest elevation known to be reached by rattlesnakes anywhere in the United States.

I have seen rattlesnakes above 10,000 feet in the High Sierra country in the Kings River drainage and also the headwaters of the San Joaquin. One point was on the ridge between Cargyle and Stairway creeks in the Sierra National Forest, south of Iron Mountain. Another location was near Loper Peak west of Woodchuck. The area near Iron Mountain is close to 11,000 feet; whereas the Loper Peak area is a little under 10,000. A third point where a rattler was recently seen was at Goodale Pass, southwest of Red-and-White Mountain. This point is a little over 11,000 feet, as near as can be determined. Also, I have seen rattlers in the Sierra Buttes country back of Sierra City, at an elevation of 8,500 feet, and just a few feet away from snowbanks in early June. *C. R. Arment, U. S. Forest Service, Susanville, Calif.*



On numerous occasions I have seen rattlesnakes near or at the summit of Sherman Peak, Sequoia National Forest. The elevation of this mountain is 9,996 feet. *E. L. Shellenbarger, U. S. Forest Service, Lone Pine, Calif.*



The highest elevation at which I have observed rattlers was 9,974 feet on Sherman Peak in the Sequoia National Forest. *Robert H. Crow, U. S. Forest Service, Springville, Calif.*



Near Lake Neall, Tuloumne County, at an elevation of 9,600 feet—we checked this at the time as it was felt that it was high for rattlesnakes—we found the largest rattler that we had seen in the Yosemite. *Albert C. Hawbecker, Madera, Calif.*

In the Kings River and other areas of the southern Sierra Nevada, in addition to the high points mentioned by my correspondents who have already been quoted, I have had a number of reliable reports of rattlers at between 9,000 and 10,000 feet, including Alpine Creek at 9,000 feet, near Kaiser Pass at 9,000 feet, near Florence Lake at 9,400 feet (Michener, 1935, p. 50), and near Lower Rac Lake at 9,500 feet, Fresno County; on Mineral Peak at 9,000; on Kern Peak, Toowa Range, at 10,000 feet, Tulare County; on Hoffman Peak at 9,000 feet, Mariposa County; and at Forsyth Pass at 9,800 feet, Tuolumne County.

Charles M. Bogert has advised me of a northern Pacific rattler killed above Sally Keyes Lake, Fresno County, in the Sierra at 11,000 feet. The lake is at elevation 10,175, and several nearby peaks exceed 12,000 feet. R. T. Moore, who collected the snake, saved the rattles so the identification is unquestioned.

*Southern Pacific Rattlesnake* (*C. v. helleri*).—The southern subspecies has less opportunity to show its high-altitude proclivities than does its northern relative (*C. v. oreganus*), since the areas above 10,000 feet in the southern ranges are quite limited compared with those in the Sierra Nevada. But there is no doubt that *helleri* does reach an altitude well over 10,000 feet in the San Jacinto and San Bernardino mountains of southern California. Joseph Ewan (1932, p. 36) reported a southern Pacific rattlesnake at not to exceed 20 feet from the peak of Mount San Jacinto, elevation 10,805 feet.

Rattlesnakes have been found in the Big Bear Lake and upper Santa Ana River areas and drainages up to an elevation of 10,000 feet. They are more prevalent on the desert slopes of Big Bear Lake than in the timbered or brush areas. *D. M. Tucker, U. S. Forest Service, Minnelusa, Calif.*

The southern Pacific rattlesnake seems to have a proclivity for climbing to the tops of rocky peaks. Besides Ewan's report of one at the top of Mt. San Jacinto, Winfield H. Line told me of finding one under the fire-observation tower on the top of Tahquitz Peak (altitude 8,826); and I, myself, caught one under the wooden observation platform on the peak of Cuyamaca, the second highest point in San Diego County (6,515 feet).

*Arizona Black Rattlesnake* (*C. v. cerberus*).—This rattler has been collected at a number of high points in central Arizona, including Manning Camp, Rincon Mountains, at 8,000 feet; K. P. Creek, White Mountains, at 8,200 feet; Mt. Lemmon, Santa Catalina Mountains, above 8,000 feet; and the San Francisco Mountains at about 10,000 feet (Coues, 1875, p. 605). It is possible, although not known to be a fact, that either the northern blacktail (*C. m. molossus*) or the Arizona twin-spotted rattler (*C. p. pricei*) might reach a higher altitude on Mt. Graham (10,516 feet) in the Pinalenos than does *cerberus* in the San Franciscos, in which case Arizona would be the only western state wherein the altitude record is not held by some subspecies of the western rattler (*C. viridis*). But *cerberus* is also found on Mt. Graham, as well as on Mt. Baldy (11,463 feet) in the White Mountains, where neither *m. molossus* nor *p. pricei* occurs; so that it could reclaim its laurels here, where the climate is not so severe as on the more northerly San Francisco peaks.

*Mexican Dusky Rattlesnake* (*C. triseriatus*).—The altitudes achieved by the two Pacific rattlesnakes in California—10,000 to 11,000 feet—are considerably exceeded by the dusky rattlesnake in Mexico. The highest of which I have heard was collected by Paul D. R. Ruthling on Mt. Orizaba (Citlaltepēt) at 14,500 feet or above. He has thus described a collecting trip, first to Ajusco and then to Orizaba:

Ajusco Peak rises to a height of over 14,000 feet above sea level. The little rattler, about which you inquired, was not found on the summit, but somewhere, possibly 1,000 feet below, or roughly at an elevation of about 13,000 feet above sea level. It was found among patches of snow in spots where the *zacatón* or bunch grass, of which brooms are made, grows profusely. The snake was not in the snow, but, as you know, at high altitudes when the radiant heat of daytime strikes directly from the sun, it may be very warm, even in the vicinity of snow patches, whereas in the more shady spots nearby, the snow may linger indefinitely.

Another specimen of *C. t. triseriatus* was found under very similar conditions on the slopes of the Pico de Orizaba. We, with our guide and horses, were lost at night trying to reach the sulphur-gatherers' cave, a camping place slightly below timber line, and had to

camp in the forests on the slopes of the mountain. When I awoke next morning, my blankets were lightly covered with snow. The other members of the party hugged a huge fire and couldn't sleep that night on account of the cold. Next morning, we reached the cave and rested all day. On the following morning, after a good sleep in the cave, we started for the summit of Orizaba. At about the edge of timber line, in a very sparsely vegetated area, rocky but with abundant tufts of *zacatón*, typical at these high altitudes, we discovered another of these little rattlers when the sun had warmed up the ground after a slight snow-fall the night before. This was at about 3,000 feet below the crater (elevation 18,696 feet), I should judge at about 15,000 feet elevation. From there on up, there were no trees, just rocky slides, and plenty of big snow fields.

Gadow (1905, p. 226; 1908, pp. 56, 61, 513) also mentions *triseriatus* on Orizaba, where he records one at 12,500 feet or slightly higher. He states (1905, p. 197) that the tree line is at about 13,500 feet, beyond which there are tussocks of grass. The snow line is at about 14,500 feet. The Museum of Vertebrate Zoölogy, University of California, has a specimen from about 11,000 feet on Popocatepetl. Mertens (1930, p. 160) mentions a specimen taken at about 13,500 feet on Mt. Ajusco.

The northeastern or Queretaran subspecies of the dusky rattlesnake (*C. t. aquilus*), although also a mountain form, does not reach the altitudes attained by *C. t. triseriatus*. However, it has been collected at 6,900 feet near Alvarez and 7,400 feet at Cerro Conejo, San Luis Potosí; 6,900 feet at Cadereyta, Querétaro; and at 8,000 feet above Jacala, Hidalgo.

Although *C. t. triseriatus* attains higher altitudes than *C. v. oreganus*, the latter may actually have a greater vertical range, since, in California, it occurs from sea level to 11,000 feet, and may, indeed, go slightly below sea level on the desert flank of the Santa Rosa Mountains in Riverside and Imperial counties. But *t. triseriatus*, a mountain form, has not yet been collected below 4,870 feet (Jalapa, Veracruz).

## HABITAT PROPENSITIES

In the following pages I shall cite the comments of some of my correspondents on the habitat preferences of the rattlesnakes, first in verification of some of the general requirements that I have discussed, followed by observations on individual species. One caution is necessary in judging these statements on preferred habitats. Where rattlers den for the winter and bask in the sun during a lying-out period, just before entering hibernation in the fall or dispersing in the spring, their numbers are so great, compared with the few found scattered throughout the summer ranges, that the environment at the dens is likely to be stressed at the expense of the summer ranges, although the latter are the real scenes of rattlesnake activity.

Several correspondents comment on the rather sharp lines that may occasionally be found between areas inhabited by rattlesnakes and those that are not. Some of these boundaries, which appear to act like barriers, seem quite inexplicable:

In every country inhabited by rattlers there are areas where none apparently occur. Whether there is some natural enemy or just some condition generally distasteful to these reptiles,

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I do not know. Where I was raised in upper Okanogan<sup>a</sup> County, Washington, there was such an area, extending for miles along one side of a small river, the Methow, where no one ever saw a rattlesnake, whereas on the other side they were uncomfortably plentiful. *F. F. Wehmeyer, U. S. Forest Service, Heppner, Oreg.*



The borders of rattlesnake territories appear to be quite abrupt, usually along the watershed between an arid section and one with greater rainfall, and accordingly more timbered. For instance, at Vernon, in the Okanagan<sup>a</sup> Valley in British Columbia, there are plenty of rattlesnakes, but ten miles away at Armstrong they are entirely absent. *C. F. Kearns, British Columbia Game Department, Nelson, B. C.*



I have often wondered why rattlesnakes are so numerous in certain areas, while in adjacent places similar in climate, altitude, and cover, there are none. A good example of this is the area at the head of the Yuba River in the Tahoe National Forest. Here snakes are numerous around Sierra Buttes Lookout, close to an elevation of 9,000 feet, but in the Lakes Basin country of the Plumas Forest, a short distance away, there are no rattlers at a much lower elevation, although the area surrounding it on all sides carries a moderate population of these snakes. *Norman J. Farrell, U. S. Forest Service, Shasta, Calif.*



Up the creek, these snakes are so plentiful that a rocky point in the canyon is called Rattlesnake Point. Just a few miles away, an area of many square miles apparently has no rattlers. A cowboy who has handled the cattle in this area for years tells me he has never seen a rattler in this section. It is somewhat higher there than the first-named place where the rattlers are common, but I have seen lots of rattlers at considerably higher elevations in Idaho and Wyoming. *Glen R. Jones, U. S. Forest Service, Bridgeport, Calif.*



Rattlesnakes are quite numerous in parts of the San Luis Valley. They seem limited quite definitely to certain particular areas. No strays are found beyond these areas. *M. A. Shoeman, U. S. Forest Service, Antonito, Colo.*



For reasons that I do not know, rattlesnakes are found to be much more numerous in some sections than in others where the conditions are quite similar. *Glenn Flathers, U. S. Forest Ranger, Camp Crook, S. Dak.*



Rattlesnakes here have very distinct ranges. There are four areas in which they always are present, but other areas with the same terrain have none. *John W. Warren, U. S. Forest Service, Hamilton, Mont.*

That food supply is often a major factor in limiting rattlesnake ranges is obvious. The following observation by Frank F. Gander of Escondido, California, refers to two subspecies of rattlesnakes, the San Lucan speckled rattlesnake (*C. m. mitchelli*) and the San Lucan diamondback (*C. r. lucasensis*), specimens of which were found in the Magdalena Plain of Baja California, in an area much more arid than that comprising most of their ranges:

This morning when I started deer hunting, I saw two places where rattlers had been coiled. One was near camp, and so this evening, Huey and I hiked over there and looked for the rattler. We found it just coming out of a hole. This snake was long and slender, and when opened for pickling was found to have nothing in the entire alimentary tract. Later at another point, we found another rattler coiled; it was extremely emaciated and easily captured. The condition of these two snakes emphasizes the fact that life here is at low ebb. About half the vegetation is dead, and the rest half-dead. A very light rain since we passed here before has been the only precipitation this year.

<sup>a</sup> The Canadian and American spellings differ.

Several answers to my questionnaires comment on the absence of rattlesnakes from agricultural lands, where they have either been driven out by persecution, or the conditions may have been made distasteful to them. This situation is also mentioned elsewhere (p. 1023).

Rattlesnakes have been observed in the foothills and mountains all around Upper Lake and throughout Lake County. Very few are found in the valley-bottoms or the level agricultural land adjoining Clear Lake. They seem to avoid entirely the more moist agricultural land. *W. C. Meyer, U. S. Forest Service, Upper Lake, Calif.*



When the whites first settled here, rattlesnakes ranged over this entire section, except at the higher elevations. But continuous killing of the snakes and the cultivation of wheat, have driven them out of large areas. One district still has a few rattlesnakes, out in what we term the "sands." This is a large strip south of the Columbia River, too arid and with a soil too light for cultivation. *F. F. Wehmeyer, U. S. Forest Service, Heppner, Oreg.*



Rattlesnakes occur only in the sagebrush desert portion of the country. None are found in the irrigated farming districts. *Paul J. Shank, Ashton, Idaho.*



Rattlesnake distribution in the state of Iowa is very spotty. There are counties where they are common, adjacent to other counties where few, if any, occur at present. For those not familiar with the state, it is difficult to visualize the gross changes brought about by human occupation. Roughly, 95 per cent of the state's area has been under the plow and most of the rest is made up of cities, villages, and wooded pastures—usually on sloping land. Probably less than half of 1 per cent is in ungrazed and uncultivated land; what little there is, is made up principally of second-growth timber and marshes. Therefore, for an animal to survive in any numbers it must adapt itself to the changed conditions. From my observations I judge that the massasauga (*S. c. catenatus*) is unable to make this adaptation. The limited pockets of this species are now confined to the relatively undisturbed areas—especially a few small tracts of unplowed grassland in the southern part of the state. The timber rattler (*C. h. horridus*) retains a relatively wide distribution, and since its habitat—wooded slopes, usually with boulders and rock outcrops—is the least suitable for human use, it has suffered less, although even of this subspecies present populations are probably but a fraction of those of a century ago. *Reeve M. Bailey, University of Michigan, Ann Arbor, Mich.*

Allyn (1937, p. 220) aptly describes the effects of agricultural and industrial developments on the rattlesnake population when he says: "The straggling remains of three species of poisonous snakes still inhabit certain sections of Indiana." Even annual changes in weather are said to modify rattlesnake ranges.

Weather conditions during the summer season have a considerable effect upon the range of these reptiles. The past season having been quite wet and cold, this naturally held the snakes to a lower level than would have been the case during a dry period in which they are found at higher elevations. *F. L. Archer, U. S. Forest Service, Lander, Wyo.*

Many of the persons to whom my inquiries were addressed merely replied that no rattlesnakes occurred nearby. This was, of course, useful information in plotting ranges. A few gave their reasons for believing rattlers absent; of these the following are examples:

There are no rattlesnakes here; the climate is too damp. *Warren M. Forsyth, Saint Helens, Oreg.*

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The altitude and rigorous winters here eliminate rattlesnakes. *Laurence B. Carr, Soda Springs, Idaho.*



The altitude here in Gunnison County is too high and the summer temperature too cold for rattlesnakes. *Tom C. Hartman, Gunnison, Colo.*



The altitude here is too high for rattlers. *E. C. Peabody, Breckenridge, Colo.*



The elevation here (6,500 to 7,500 ft.) is apparently too high for rattlesnakes. *Charles H. Thompson, Evanston, Wyo.*

### CHARACTERISTIC HABITATS OF SUBSPECIES

The following descriptions of the particular kinds of habitats in which the various species of rattlesnakes are most often found, are quoted from observations communicated to me by many correspondents, or have been taken from published articles, or from my own field notes. Some typical habitats are shown in figures 8:1 to 8:8. I should mention again that observers are likely to stress the nature of the surroundings in which rattlers are seen concentrated at their dens during the brief lying-out periods of spring and fall, as compared with their summer ranges, when they are scattered, largely nocturnal, and therefore less often encountered. This is particularly true of the subspecies of the western rattlesnake, *C. viridis*, and other forms inhabiting areas with severe winters.

*Eastern Diamond Rattlesnake (C. adamanteus).*—This large rattlesnake is a low-land form, restricted to the Florida peninsula and the coastal plains from extreme eastern Louisiana to North Carolina. Within this area it is said to live in almost any available type of habitat, except especially wet places. Upon this my correspondents observe:

Most of my experience with rattlesnakes has been in the Ocala Forest, Florida, better known as the "Big Scrub," where I was a ranger for six years. The Big Scrub is covered with sand pine, saw palmetto, and scrub live-oak; also, other dwarf varieties of hickory, bay, etc. In the flat-woods type there are palmettos and gallberry. Where the scrub type changes into swamp, the diamondback rattlers seem to live up in the scrub in the daytime, where they lie under saw palmettos in the shade. In the late afternoon they start for the swamp and return at dusk.

I would say that the diamondbacks prefer dry country such as the Big Scrub. Occasionally they are found in swamps. They are pretty common in hammocks [hardwood thickets] and palmetto thickets. You find them occasionally in flat woods; also in long-leaf pine woods. But they like the palmetto country best, as they have good cover there, and places to look for prey. *Joseph T. McCullough, U. S. Forest Service, Brooklyn, Miss.*



Diamondbacks are mostly found in hammocks adjacent to creeks and beaches. *Herbert Kulp, Niceville, Fla.*



The hammock where we hunted is typical of the hardwood hammocks in being on a limestone foundation. The whole hammock is honeycombed with subsurface connecting sink-holes, making a maze of tunnels with surface-openings throughout the hammock. In and on these fern-studded, hardwood-covered hammocks, occupying relatively high ground of the Everglades, *C. adamanteus* is to be found in considerable numbers. First I came upon a cast-off skin, wet, lying in dead leaves of the "woods" floor near several sink-holes. Careful scrutiny of the surrounding few yards disclosed two adults coiled beneath a fern. They were nearly impossible to see from an upright walking position. The fern, various twigs

and vines, coupled with the snakes' concealing coloration blending with the dead leaves of the hammock floor, effectively hid these comparatively large rattlesnakes. The male measured 4 feet 7 inches, the female 5 feet 1 inch. *Charles H. Lowe, Jr., Tucson, Arizona, writing from Florida.*

John M. Frazier has written me that he found eastern diamondbacks numerous in the long-leaf pine belt of Mississippi; and Robert E. Gordon says that in Wilcox County, Georgia, they were prevalent in pine barrens, and in scrub palmetto on a sandy soil.

Various published accounts have described the haunts of the eastern diamondback. Loennberg (1894, p. 335) thought them more plentiful on the Florida Keys and along the coast than back in the interior. Beyer (1900, p. 29), writing of Louisiana, stated that the diamondbacks were being thinned out by the drainage of swamps and the clearing of forests. His prophecy has proved accurate, as these snakes are now rare, if not entirely exterminated in eastern Louisiana. He stated that diamondbacks prefer the vicinity of water. They have the habit of coiling beside a fallen tree, and there have been many narrow escapes when persons have stepped over logs. Geare (1903, p. 118) thought *adamanteus* to prefer damp, shady spots. Reese (1910, p. 365) reported them found most often in scrub palmetto clumps. Conant and Bridges (1939, p. 143) say that the diamondbacks in the daytime seek cover under the broad leaves of the dwarf palmetto, beside stumps or logs, or in burrows.

Allen and Merryday (1940, p. 234) prefer to hunt for them in the holes of the gopher tortoise (*Gopherus polyphemus*), where they take refuge in cold weather or in case of forest fires. A ruse used by collectors is to cover the holes, for when they return and remove the covers, the snakes usually come out. All writers agree that the eastern diamondback often seeks refuge in the burrows of the gopher tortoise. Carr (1940, pp. 12-27, 95) says that in Florida the eastern diamondback is partial to dry situations; its preferred habitat is palmetto flatwoods. Other habitat associations in which it occurs frequently or occasionally are high pine, wire-grass flatwoods, low mesophytic and upland hammocks, salt marshes, and bayheads. Fannye Cook (1943, p. 52) reported that in Mississippi many were killed when a virgin pine forest was harvested. In summer they seek shady spots near water; in winter they are more often found in gopher-tortoise holes, caves, or in rock crevices on dry hillsides.

Davis and Brimley (1944, p. 9) state: "This species seems to like all areas within its geographic range whether sand, pine ridges, or deep swamps. . . . Favorite hiding places are under dwarf palmettos, rotting stumps and hollow trees, as well as in burrows or dens of other animals." Snyder (1945, p. 174) says that in Alabama these rattlers are usually found in wild, brushy areas. Fourteen were killed in one day by the 66th Infantry in a clearing in open, dry woods. The clearing was well filled with logs left from lumbering operations some years before.

Allen and Neill (1950a, p. 10) summarize their wide experience with this largest of rattlesnakes by stating that it is most often found in areas of palmetto, flat woods, pine woods, "scrub," live-oak hammocks, or thickets, and abandoned fields. Neill recently informed me that he would describe the habitats most suitable to this species as high pine (long-leaf pine and turkey oak) and rosemary "scrub." These are drier areas than most of the surrounding country. Others who have



Fig. 8:1. Typical habitat of the timber rattlesnake (*C. h. horridus*) at Jacobs Rocks, near Laurel Hill, Westmoreland County, Pennsylvania. (Photograph by Stephen H. Harwig.)



Fig. 8:2. Thunder Butte, Ziebach County, South Dakota, site of a den of the prairie rattlesnake (*C. v. viridis*). (Photograph by Howard K. Gloyd.)



Fig. 8:3. Giant cactus and mesquite, Tanque Verde Ranch, near Tucson, Pima County, Arizona. Habitat of the western diamond rattlesnake (*C. atrox*) and the Mojave rattlesnake (*C. s. scutulatus*). (Photograph by Laurence M. Huey.)



Fig. 8:4. Cactus and rocky hills, near Papago Well, Pima County, Arizona. Habitat of the western diamond rattlesnake (*C. atrox*), the Sonoran Desert sidewinder (*C. c. cerobombus*), the northern black-tailed rattlesnake (*C. m. molossus*), and the Mojave rattler (*C. s. scutulatus*). (Photograph by Laurence M. Huey.)



Fig. 8:5. Borrego Desert, San Diego County, California. Ocotillo and other thorny shrubs. Habitat of the Colorado Desert sidewinder (*C. c. laterorepens*), the southwestern speckled rattlesnake (*C. m. pyrrhus*), and the light-colored, desert phase of the red diamond rattlesnake (*C. r. ruber*).



Fig. 8:6. Mountain forest, San Diego County, California. Habitat of southern Pacific rattlesnake (*C. v. helleri*).



Fig. 8:7. Granite and chaparral in the coastal foothills, San Diego County, California. Habitat of the southwestern speckled rattlesnake (*C. m. pyrrhus*), the red diamond rattlesnake (*C. r. ruber*), and the southern Pacific rattlesnake (*C. v. helleri*).



Fig. 8:8. Cape San Lucas, Baja California del Sur, Mexico. Habitat of the Lower California rattlesnake (*C. e. enyo*), the San Lucan speckled rattlesnake (*C. m. mitchelli*—this is its type locality), and the San Lucan diamondback (*C. r. lucasensis*). (Photograph by Laurence M. Huey.)

recently discussed the habitat are Haliburton (1935, p. 67), who says diamond-backs are not common in the Everglades, where there is too much water; Allison (1946, p. 46); Allen (1949a, p. 70); Babbitt and Babbitt (1951, p. 79); and Teale (1951, p. 47).

*Western Diamond Rattlesnake* (*C. atrox*).—This large snake, in its range from Arkansas and central Texas west to the Colorado Desert in California, inhabits a wide variety of terrain. But usually it is found in dry—even arid—country, such as brush-covered plains, dry washes, sandstone outcrops, or mesquite-crowned dunes. So it deserves the name by which it is sometimes called—the desert diamond rattlesnake.

Western diamond rattlesnakes like brushy, rocky country, and rolling hills best. Once in a while, they will be found in grassy meadows or fields. They are inactive during the hot parts of the day, and do most of their feeding late in the evenings. Hound hunters in this area prefer not to hunt at night, for this is a good time for humans and dogs to be bitten. In clearing 10,000 acres of cactus and brush in Shackelford County, Texas, one rancher killed 1,200 rattlers. Another ranchman killed 60 rattlers to the section, in clearing off cactus and brush. *John R. Wood, Brownwood, Tex.*



Rattlesnakes do not seem to have much preference as to type of country they inhabit; if there is any preference, it seems to be for the moderately rocky, rough and brushy type. They are to be found during the hotter periods in moist shady areas along streams, and adjacent to such lakes as Roosevelt, Apache Canyon, and Sahuaro in the Salt River chain. In the spring and early summer they are numerous in the low country adjacent to the desert, which is largely a decomposed granite and black-malapai formation. Also, they are frequently found in irrigated fields, which are mostly of a red clay and sand composition. *A. L. Alexander, U. S. Forest Service, Roosevelt, Ariz.*



The following applies to the area of about 500 acres included in Montezuma Castle National Monument at an altitude of approximately 3,200 feet. Part of the monument lies along the course of Beaver Creek, a tributary of the Verde River, and the rest is comprised of mesquite-covered terraces bordering the river, of limestone hills covered principally with creosote brush (*Larrea tridentata*), and Mojave thorn (*Canotia holacantha*). Rattlesnakes are often seen in these surroundings, but I doubt whether they could be called numerous. The three species recorded here are, in the order of their abundance, western diamonds (*C. atrox*), northern blacktails (*C. m. molossus*), and Mojave rattlesnakes (*C. s. scutulatus*). *Homer F. Hastings, Montezuma Castle National Monument, Camp Verde, Ariz.*

But although the western diamond rattlesnake does occur in Arizona in such hilly or mountainous areas as those around Montezuma Castle, Mayer, and Roosevelt Lake, it is primarily a lowland form, a dweller of plains and desert flats. About Tucson I found *atrox* moderately common, mostly in mesquite areas, both across the Santa Cruz River near San Xavier Mission and in the rolling country toward Oracle Junction. There is also much creosote bush and some cactus in the latter section. In central Arizona, southwest of Prescott, it was common at such points as Kirkland, Hillside, Date Creek, and Congress. This is a country of mixed grassy plains with rock outcrops, and barren, rock-strewn hills interspersed with some chaparral and cactus. Toward the south there is much mesquite. The

western diamonds, although found in all situations, seemed commonest in the dry washes. At Mohawk, a professional collector said he found most of his specimens in sandy areas, particularly under the overhanging banks of the Gila River.

At Blythe, Neighbors, and Ripley, in eastern Riverside County, California, and across the Colorado River at Ehrenburg, Arizona, the western diamond rattler is occasionally found in irrigated areas and among the mesquite and willows of the river bottom, but it is more frequently met in more arid situations, such as the dry washes of the tributaries. At Indian Wells, in central Riverside County, it is significant that a professional collector, who maintained a roadside show for tourists, and also shipped out large numbers of snakes, collected most of his western diamonds in the mesquite-crowned sand dunes. He made a practice of following their night tracks in the early morning. They were not absent in the nearby irrigated Coachella Valley but were less plentiful there. They seem not to have invaded the adjacent tumbled rocks of the desert foothills of the San Jacinto Mountains, immediately to the west. Here they are replaced by the red diamond rattler (*C. r. ruber*), which, although a closely related subspecies, is quite different in character and temperament.

Among the kinds of territory in which I have found western diamonds, the following have been recorded in my diary: Mesquite, dense creosote brush, brushy desert, brush lining an irrigation canal. Lee W. Arnold, collecting in the vicinity of Tucson, Arizona, found seven *atrox* in mesquite compared with two in creosote bushes. At Komatke, 12 miles southwest of Phoenix, they were in a salt bush (*Atriplex*) association, bordering a sandy desert road. Ruthven (1907, p. 593) collected *atrox* in southern Arizona in a creosote-bush association. Ortenburger and Ortenburger (1926, p. 117) found it confined to plains and washes in a mesquite association. This was in the vicinity of Tucson.

Mosauer (1932d, p. 16) found western diamonds in flats in the Guadalupe Mountains of New Mexico. In the Colorado Desert (1935b, p. 21) he found them to inhabit thickets of mesquite and stands of desert willow. They did not often venture into the open. Humphrey (1936, p. 329) found them most prevalent in the vicinity of Tucson, Arizona, at altitudes of 2,800 to 3,400 feet in the better grassed areas and up to 4,000 feet in brushy areas. E. H. Taylor (1936, p. 497), collecting in Sonora, came upon *atrox* on gravelly flats along the seashore, and in sand piled up by the waves, where sand beach and shrubs met. Here there were many rodents. Milstead, Mecham, and McClintock (1950, p. 544) found *atrox* to favor mesquite and creosote bush in Terrell County, Texas. The most southerly colonies of *atrox* in mainland Mexico are found in Oaxaca, in areas of tropical thorn forest or tropical savannah as defined by Leopold (1950, pp. 514, 515).

Although this rattlesnake, over most of its range, is an inhabitant of arid lowland areas, it occasionally reaches altitudes well over 5,000 feet. Near Otowi, Sandoval County, New Mexico, specimens were collected by C. M. Bogert at 6,000, 6,200, and 7,000 feet. It has been recorded above 5,000 feet near Fort Huachuca in Arizona. It apparently reaches its maximum altitude in San Luis Potosí, Mexico, where it has been collected at 7,000 feet near Illescas, and at 8,000 feet near Alvarez. It is found below sea level in the Salton Basin of Riverside and Imperial counties, California, probably down to -200 feet.

*Mexican West-Coast Rattlesnake* (*C. b. basiliscus*).—This large rattler is usually, but not entirely, restricted to the coastal plain of western Mexico, from extreme southern Sonora to Colima and northwestern Michoacán. Goldman (1951, pp. 135, 253) refers to this as a part of the Arid Tropical Zone. At Colima this rattlesnake subspecies is apparently quite plentiful, for numbers are shipped to the United States each year, where, in the snake-show trade, they are known as Mexican green rattlers. (They are predominantly red when young, but olive green when fully adult.) The coastal plain at Colima is described by Goldman as being largely treeless and covered with short grass but having scattered clumps of mesquite, acacias, and other thorny bushes and small trees, as well as an abundance of large cacti. If classified according to the vegetation zones of Leopold (1950, pp. 515, 516), the range of *basiliscus* is mostly in the tropical thorn forest, with an extension up into the tropical deciduous forest.

Although the coastal subspecies (*C. b. basiliscus*) may reach moderate heights—a specimen is recorded from near Apatzingán, Michoacán, which has an altitude of about 3,200 feet—the Oaxacan subspecies (*C. b. oaxacus*) probably reaches a more impressive altitude, since one of the 2 known specimens was taken at or near the city of Oaxaca (Oaxaca de Juárez), Oaxaca, Mexico, which has an altitude of 5,500 feet and is surrounded by mountains. This is an area of pine-oak forest.

*Sidewinder* (*C. cerastes*).—Sidewinders prefer the sandy areas of the desert, yet they are by no means restricted to sand, for they are often found in places where the surface is baked hard, and where stones are strewn about. But they do occur in the most extreme arenaceous areas and they are rare or absent on rocky hill-sides where there is no soft ground nearby. If the territory is diverse, sidewinders are more likely to be found in the flats, particularly about sand hummocks or along sandy washes.

For example, in eastern San Diego County they are plentiful along the sandy wash of San Felipe Creek, from Yaqui Well to The Narrows and beyond; but up the rocky side-canyon of the Sentenac they have never been taken, although this territory has been hunted assiduously. Nor are they present in In-Ko-Pah Gorge, Imperial County, west of Coyote Well. But where they are able to follow washes and thus reach isolated valleys, they will persist there, as is the case at La Puerta, or Mason Valley, of eastern San Diego County. In flats of this kind they are by no means restricted to places where the soil is loose or sandy. I should say that the ideal territory for the sidewinder comprises desert flats with scattered brush, and where sand hummocks, crowned with mesquite, or sandy washes are prevalent. And they can exist in terrain that is entirely sand, as shown by their presence in the sand hills in Imperial County, some 20 miles west of Yuma, where the strip of dunes is fully 5 miles wide. I have found them in the sands of Death Valley.

Although sidewinders usually seek mammal holes in the heat of the day, they occasionally rest in shallow depressions which they themselves make in the sand, and here they may stay until the heat becomes uncomfortable (fig. 7:4). I have found them coiled this way several times. I particularly remember one settled in loose sand so that the ridge of its back was flush with the surface; this was in

Pushawalla Canyon, Riverside County, June 1, 1940. This semiburial has been described by Ditmars (1923, p. 29), Mosauer (1932a, p. 74), Gloyd (1937, p. 125), and Cowles (1945, p. 221). The same bedding-down method, although attributed to *tigris* (= *stephensi*) by Heller in Meek (1905, p. 16), was probably based on observations of sidewinders. Cowles believes that in the rare instances when sidewinders are found nearly or completely covered by sand, the covering has usually been effected by the wind rather than by the shaking-down motion of the snake as it hollows out its depression. Dorothy Hogner (1938, p. 109) was told a mythical yarn to the effect that sidewinders bury themselves in the sand with only their heads sticking out, from which position they jump out at the unsuspecting passer-by.

Sidewinders are occasionally reported in the bottoms of abandoned mine shafts and dry wells. Except in the case of relatively shallow depressions, they are no doubt there by accident. Dannaldson (1938, p. 7) reports sidewinders in rats' nests, the debris of deserted cabins, the dried carcasses of dead cattle, mine shafts, and tortoise burrows. Johnson, Bryant, and Miller (1948, p. 274), in the vicinity of the Providence Mountains of San Bernardino County, California, found *cerastes* most common in low, hot, valley bottoms, especially where the soil was of a fine, wind-deposited type. The three sidewinder subspecies do not appear to differ to any degree in the character of the country inhabited. Always it is an area of extreme aridity and high summer temperatures, with some sand in the vicinity, either wind-blown or freshet-carried.

It is not known whether the sidewinder ever reaches an altitude of 5,000 feet, although it may in a few places. The Mojave Desert subspecies (*C. c. cerastes*), which occupies a generally higher country than the others, is found at least up to 4,500 feet in Nevada (Quartz Spring, Lincoln County, and Sarcobatus Flat, Nye County) and 4,200 feet in California (near Bishop, Inyo County, and Chalfant, Mono County). Two subspecies occur below sea level: *C. c. cerastes* in Death Valley, where it has been reported at -250 feet near Furnace Creek Ranch; and *C. c. laterorepens* along the shore of the Salton Sea in Riverside and Imperial counties, California, at an elevation of about -240 feet.

*Neotropical Rattlesnake* (*C. durissus*).—First as to the Central American subspecies (*C. d. durissus*): March (1928, p. 55) said that the Central American rattlesnake is not found on the coastal plain, but rather in the rolling or mountainous interior of Honduras and Guatemala. He wrote:

Along the Chamelecón and upper Ulua rivers the cascavel is found on the unwooded mountain ranges and in the tall grass (often as high as a man) of adjacent potreros . . . at El Plan, El Sato, and Cofradia they are found in the potreros and on the rocky hillsides. They are rarely found on the low, moist bottom lands. . . . In the neighborhood of Pimiento, on the Ulua River, the cascavel is occasionally met in the cane fields. . . . Their favorite haunts, however, are the higher localities, and the occasional specimens found in the lowlands are, I think, of accidental occurrence.

Stuart (1954, p. 20) reports that, in Guatemala, *durissus durissus* is an inhabitant of a subhumid corridor that extends from the Tehuantepec region of Oaxaca, Mexico, across central Guatemala into northwestern Honduras. He refers to this rattlesnake as belonging to a xeric fauna.

H. C. Clark (1942, p. 42) states that the Central American rattler inhabits dry interior tablelands. Dunn reports this snake both on the Pacific coastal plain and in the interior highlands of Costa Rica, particularly at the higher elevations. He doubts its occurrence as far east as western Panama, for a collection of about 12,000 snakes from Panama did not include a single rattler. Picado T. (1931, p. 49) says that *durissus*, in Costa Rica, is most prevalent in brushy and rocky areas. W. Leslie Burger collected several specimens of *durissus* in Oaxaca and Chiapas, Mexico. They were found on open, wooded hillsides with much brush and tall grass, and frequent rock outcrops; also in a dry savanna with wooded arroyos nearby.

The subspecies *C. d. durissus* ascends to moderate heights; it has been collected near Comitán, Chiapas, Mexico, at 5,200 feet; near Cobán, Guatemala, at about 4,300 feet; and near Cartago, Costa Rica, at 4,760 feet.

The northwestern subspecies (*C. d. culminatus*) avoids the lowland, so far as is known. It is found in the mountainous areas of Michoacán, Guerrero, and Morelos, Mexico, at altitudes from about 2,800 feet (Acahuizotla, Guerrero) and 3,200 feet (Xochicalco, Morelos) to 7,000 feet (Omitéme, Guerrero). Davis and Smith (1953, p. 141) found it rather common in the low mountains south of Tepaltzingo, Morelos. The territory inhabited is extremely rough, and altitudes are seldom recorded with accuracy; it is referred to by Goldman (1951) as extending from the Arid Upper Tropical Zone to the Lower Austral Zone. Leopold (1950, p. 510) refers to the vegetative cover of most of the territory occupied as a temperate pine-oak forest.

The Yucatán subspecies (*C. d. tzabcan*) is a lowland rattlesnake, inhabiting the forested areas of the Yucatán Peninsula. This is a country of numerous rock outcrops, and vegetation varying from sparse to dense. Leopold (1950, p. 514) places the principal parts of the peninsula inhabited by *tzabcan* as in the tropical evergreen and tropical rain forest areas.

The last of the North American subspecies of *C. durissus* is the Totonacan rattler (*C. d. totonacus*) found on the Gulf, or eastern, slope of the Sierra Madre of southern Tamaulipas, southeastern San Luis Potosí, and northern Veracruz. This is an area of tropical thorn and tropical deciduous forests (Leopold, 1950, pp. 515, 516), but *totonacus* ranges into the temperate deciduous forest, for it reaches an altitude of at least 5,200 feet.

With regard to the South American subspecies (*C. d. terrificus*), it seems to be agreed that in a continent often erroneously thought to be mostly tropical jungle, the rattlesnakes characteristically occur in dry and arid sections. André (1904, p. 160) reported that they were common in arid districts along the north coast of Venezuela. They were not seen in the forests. W. Leslie Burger, who collected several rattlers in Venezuela, found some on the Araya Peninsula in arid areas resembling southwestern Arizona. Not only his own collecting, but such authentic data as were obtained from the natives, pointed to a desert-scrub habitat. These rattlers occur on the arid, northeastern shore of Lake Maracaibo.

Beebe (1946, p. 51) found *terrificus* rare in the jungle at Kartabo, British Guiana, where only 3 were taken in 8 seasons; it was more common in the open llanos or savannas of Caripito, Venezuela. Wavrin (1939, p. 135) reported that

in the Amazon area rattlers live in dry savannas or rocky sections. They are not found in marshes or forests subject to overflow.

In southern Brazil, according to Dr. Eduardo Vaz, of the Butantan Institute, rattlesnakes occur in dry and sandy areas. Dr. Vital Brazil (1911, p. 52; p. 61 of the French edition) reported that they occupy dry areas, with fields, rocks, and clumps of brush. Machado (1945, p. 55) found them prevalent in dry areas where there are dense thickets. The highest altitude that I have seen reported for this subspecies is 6,100 feet, on Mt. Naiguatá, Estado de Miranda, Venezuela. I presume it occurs at still higher levels in Colombia and Venezuela.

In general, it can be said that the various subspecies of the Neotropical rattlesnake, in both North and South America, are most prevalent in sections somewhat resembling our own arid Southwest. This is significant, in view of the availability of vast expanses of forest and other areas of heavy rainfall and dense vegetation.

*Lower California Rattlesnake* (*C. enyo*).—The southern subspecies (*C. e. enyo*) is most plentiful in the Cape region of Baja California from La Paz to San José del Cabo, a region generally arid, with a profusion of cacti, xerophytic shrubs, and rocks. The northern subspecies (*C. e. furvus*) occurs in the San Quintín Plain, an area much like western San Diego County, but somewhat more rocky and with a lighter brush cover.

*Timber Rattlesnake* (*C. h. horridus*).—A number of my correspondents have commented on the kind of terrain tenanted by the timber rattler, the rattlesnake of greatest interest to those living east of the Mississippi River and north of the Gulf states. I have already mentioned the altitudes at which *horridus* is found in the Appalachian Mountains.

Moderately steep, rocky ridge-tops with light ground-covering seem to be best suited to the timber rattlesnakes, as most of them are found in this kind of terrain in this section of the country. *C. B. Clark, U. S. Forest Service, Duffield, Va.*



During their active season timber rattlers spread out from their dens over considerable distances—a mile or more—going wherever food is likely to be found, but for the greater part restricting their travels to the wooded sections. Only occasionally is a rattler reported as having been found in an open field, and then rarely more than a quarter of a mile or so from the nearest wooded area. Many are found near rocky ledges. *Charles O. Handley, Fish and Wildlife Service, Blacksburg, Va.*



It has been noted that high, rocky ridges, having a southern exposure, are much used by rattlers, especially during the early spring and late fall. They are never found where the ground cover is dense, except when on the move. When found on the rocky slopes, or ridges, rattlers are usually coiled in a spot that affords some shade, even if the spot is well exposed where the rattler is lying. When found in the shady coves, the rattler prefers to lie coiled under sparse ferns, whose shadows form a good camouflage for the snake, owing to the pattern of sun and shade on the ground. These spots seem to be preferred for feeding grounds. *John H. Stanley, U. S. Forest Service, Andrews, N. C.*

Stephen H. Harwig, of Pittsburgh, informs me that in western Pennsylvania the timber rattlesnakes are most often found on the same rocky hillsides where their winter dens are located. They apparently prefer ledges that have a fairly

substantial brush cover, particularly of huckleberry. The dense shade of trees, however, is less often sought.

Most of those who have published data on the habitat of the timber rattler agree that it prefers rocky wasteland, without too dense a cover. Among these have been Morse (1904, p. 138, Ohio), T. E. B. Pope (1925a, p. 17; 1925b, p. 130, Wisconsin), Guthrie (1926, p. 189, Iowa), Babcock (1929, p. 28, New England), Hibbard (1936, p. 281, Kentucky), Conant (1938, p. 118; 1951, pp. 118, 256, Ohio), Hudson (1942, p. 86, Nebraska), Lueth (1941b, p. 21, Illinois), McCauley (1945, p. 137, Maryland), Allyn (1948, p. 13, Indiana), and Barbour (1950, p. 106, Kentucky). Several mention timber as being also frequented, but not heavy stands. Netting (1932, p. 13) says that although these rattlers prefer hills and mountains with ledges of broken rock, in eastern Pennsylvania and farther south they may inhabit sphagnum bogs and swamps, and may wander through farms in search of food. In August there is a trek from the dry ridges to the valleys for water. King (1939, p. 577) says they prefer second growth clearings, rocky slopes, and oak-pine woods in the Great Smoky Mountains National Park. Beyer (1900, p. 42) mentions their habit of coiling beside fallen logs.

Agricultural developments, timber cutting, and the encroachments of other human activities have probably circumscribed the range of the timber rattlesnake more than that of any other subspecies. It has been completely exterminated in some areas, such as in Maine (Fobes, 1951, p. 530) and on Long Island (Engelhardt, Nichols, Latham, and Murphy, 1915, p. 3), and has been greatly reduced in numbers elsewhere in its great range, where it is now almost entirely restricted to wild and primitive places. This was the rattlesnake first met by the British settlers in the northeastern states; and as early as 1744 Bartram (p. 358) commented on its disappearance from the vicinity of Philadelphia; and Kalm (1752-53, p. 132; 1758, p. 286) and Pennant (1787, p. 88) noted its decline in other populous sections. Warden (1816, p. 13) said rattlers were still common on the banks of the Potomac at Washington when he wrote. Packard (1886, p. 736) discussed their range in New England, where they still exist in isolated and scattered colonies, usually in rocky areas, in every state except Maine.

The following statements are applicable to the southern subspecies, that is, the canebrake rattler (*C. h. atricaudatus*):

Rattlesnakes like high, ridge lands but without too dense undergrowth. *J. A. Hale, District Game Warden, Boligee, Ala.*



I have never found a rattlesnake in thick grass, brush, or briars. However, they enter such places when danger is near. I have found them in thick and thin stands of timber. The covering may be very thick just above the ground, but the actual surface of the ground has always been relatively clear of any thick growth where they have been found. *Herbert P. Rice, U. S. Forest Service, Meadville, Miss.*



A logging crew killed 56 rattlers on one 40-acre tract of timber having a heavy undergrowth of palmettos in 15 days time. The snakes seem to prefer bottom lands, in swamps, as they would be called by non-Louisianians. *J. M. Sherwin, Alexandria, La.*



Previous to the building of the "Airline Highway" in the swamps three miles back from us, there was a very large colony of canebrake rattlers in a rather small area at the rear of the plantation just below us. The building of the highway through this section resulted

in killing off or dispersing this colony. It was a true canebrake thicket of cane-reeds (many people mistakenly believe that a canebrake refers to a field of sugar cane) in what is referred to here as "high ground." That is, it is about three or four feet higher than the surrounding very flat fields. Because of the wide drainage ditches which surround all fields, it would be natural to assume that the rattlesnakes of this section must cross considerable water from time to time, but this is not positive. *George P. Meade, Gramercy, La.*



Rattlers live near bamboos and under the hollow bark of dead trees, and in thick palmettos, or on the ground under deal leaves in summer. *Charles J. Boudreaux, Abbeville, La.*

Carr (1940, pp. 12, 96) states that *atricaudatus* is found in wire-grass flatwoods in northern Florida. Clark (1949, p. 260) mentions its occurrence both in creek bottoms and on rocky ridges. Allen and Neill (1950c, p. 19) list the following habitats of this subspecies: overgrown fields in abandoned farms; under the floors of deserted cabins; thickly wooded areas bordering lakes or streams; and brushy hollows full of fallen logs and rank weeds. In the hot season, they may be found in areas of heavy timber and sometimes in actual swamp. The true canebrakes are gone now, so they say; thus the common name is hardly appropriate for this rattlesnake.

*Small-Headed Rattlesnake (C. intermedius).*—This small rattlesnake occurs only in the mountains of southern Mexico. Most specimens of the eastern subspecies (*C. i. intermedius*) that I have studied were collected in the general vicinity of Las Vigas and El Limón Totalco, Veracruz, at altitudes of from 7,800 to 8,500 feet. Goldman (1951, p. 274) says there is a greater luxuriance of vegetation along this eastern border of the Mexican tableland than is present farther west in the interior. This is the tropical evergreen forest of Leopold (1950, p. 514). The maximum elevation at which this subspecies has been found is 10,000 feet on Cerro San Felipe in Oaxaca.

The Omilteman subspecies (*C. i. omiltemanus*) occurs between elevations 4,500 and 7,900 feet in the area between Chilpancingo and Omilteme in Guerrero. This is a rough and somewhat arid country, at least up to 7,000 feet, above which there is usually a more profuse vegetation. Chilpancingo is in a scrub-oak association. Omilteme is higher, amid steep mountains with a dense cover of pine and with plenty of water.

R. W. Axtell wrote me that specimens of *omiltemanus* collected by him came from rather open, pine-covered slopes at between 7,700 and 7,800 feet. Places exposed to the sunlight most of the day were preferred. None were located in the hardwood cloud-forest environment. Some specimens were found under pine logs or bark, others while sunning themselves.

*Rock Rattlesnake (C. lepidus).*—The rock rattlesnake is primarily a mountain form, and is, as its name implies, a rock dweller. With regard to the easterly subspecies, the mottled rock rattlesnake (*C. l. lepidus*), L. T. Murray (1939, p. 13) reported that it seeks inaccessible rocky places in the higher parts of the Chisos Mountains of Texas, where it has been collected up to 7,000 feet; in the Davis Mountains it has been found as high as 6,800 feet on Mt. Locke. It does not occur in the flats at the base of the mountains and is found only rarely in the mountain valleys.

In Terrell County, Texas, Milstead, Mecham, and McClintock (1950, p. 544) found the mottled rock rattlesnake in a persimmon-shin-oak association. It was largely restricted to precipitous rimrock and to a narrow strip adjacent to the base of the outcropping limestone. It was found either on bare limestone or rimrock, under rocks lying on other rocks, or under rocks lying on humus. Col. M. L. Crimmins informed me that in Real County, Texas, this subspecies was found at altitudes of from 2,000 to 3,000 feet, in rocky, dry watercourses. At sundown the snakes were lying on rocks or logs, and when disturbed took refuge under flat stones. In Mexico, this subspecies has been found as high as 9,600 feet on Cerro Peñon Blanco, San Luis Potosí.

From my correspondents the following notes are available on the westerly subspecies, the banded rock rattlesnake (*C. l. klauberi*), which is to be found in a number of mountain ranges in southwestern New Mexico and southeastern Arizona, as well as farther southward deep into Mexico:

I found one specimen of *klauberi* in Rock Creek Canyon, at about 7,000 feet, and another in Ward Canyon at 7,500 feet in the Chiricahua Mountains. The first was found near a creek bed, the latter on the edge of a rock slide. Both retreated immediately.

In the Chiricahuas, *klauberi* was found in the same situations as was *pricei*, but it was not so common as the latter. In the Huachucas their numbers were reversed, only one *pricei* being taken compared with more than 30 *klauberi*. In the Huachucas, *klauberi* was found in the same associations as *pricei* was found in the Chiricahuas, that is, principally rock slides, but also grassy mountain meadows and brush. Though not all the canyons were collected thoroughly, I believe that *klauberi* and *pricei* are equally common in the Huachucas and Chiricahuas, respectively—the west slope of the Huachucas excepted, due to associations and conditions. Only one *pricei* was taken on the east slope of the Chiricahuas, though similar conditions exist as on the west. Possibly more collecting on that slope would reveal more specimens. No specimens of *klauberi* were taken on the west slope of the Huachucas, owing to the vastly different type of country. Chaparral and steep slopes greatly hindered collecting there, and the difficulty in collecting really was an important factor, as the crest itself was no short distance from camp. But in the rocky canyons on the east slope the collecting was excellent. *Lawrence H. Cook, San Diego, Calif.*



In the Chiricahuas the banded rock rattler is met with on the fairly open slopes, with some ground cover, and in rock slides and outcrops at about 7,000 feet and above. It is a very timid snake. *J. T. Wright, Tucson, Ariz.*



Carlton Perkins and I had the following experiences collecting the banded rock rattlesnake, in Ramsey Canyon, Huachuca Mountains, Arizona, in 1933: On July 20, we found a small one sunning itself on a rock at the bottom of a ravine (9:30 A.M., air temperature 90° F.). Five minutes later another, slightly larger, was found on pine needles on a ledge near the bottom of a cliff. I failed to see this one and stepped on the edge of its body, upon which it struck my shoe. Another was found lying beside the trail (2 P.M., 95° F.). Two days later we found one that was blind and dull from the skin-changing process. It was under loose rocks on a shelf about half-way up a cliff. It rattled, thus giving itself away, when we walked over the rocks (9 A.M., 80° F.). Another was found lying beside the trail at noon (85° F.). It sought refuge under a rock. On July 23, at 2:05 P.M. (75° F.) we found one at 6,000 feet sunning itself beside a boulder at the base of a cliff. Next day at the same altitude we found another under a flat boulder. It rattled when the boulder was walked on (9 A.M., 75° F., windy). On July 24, a small one was found in the open at 6,000 feet; it rattled and crawled under a flat rock (9:45 A.M., 75° F.). On July 26 we found a pair at the B. and A. Mine in upper Ramsey Canyon. They were sunning themselves beside a small pile of

loose rock on the shelf of a cliff. Both rattled; one retreated into a hole and the other did likewise, but in so doing only concealed about a third of its length (10 A.M., 75° F., 6,700 feet). At 10:30 another advertised its presence by rattling when we stepped on loose rocks under which it was hidden. Several yuccas were alongside the rocks. At 2 P.M. (75° F., 5,700 feet), a small one was found on the rim of Box Canyon, lying in the trail. *A. Pierce Artian, Los Angeles, Calif.*

Dr. Henry Skinner, in 1905, was probably the first to employ the method of collecting these rock-inhabiting snakes that most subsequent collectors have adopted—that is, by rapping on rocks under which they may be hidden, thus causing them to rattle and disclose their presence (W. Stone, 1911, p. 232). Gloyd (1937, p. 127) found these little rattlers in piles of rock, sunning themselves on the tops of flat rocks, or beneath stones or pieces of bark. Although the concealed snakes would sometimes rattle, he reported the sound so faint it could be heard with difficulty.

Woodin (1953, p. 294) collected a number of specimens of *klauberi* in the Huachucas at elevations of 5,300 to 7,000 feet. Most of them were found in rock slides, but a few were in other rocky areas, and one was in a grassy space far from rocks. The maximum altitudes that I have seen recorded for this subspecies are 7,200 feet in the Huachucas, 7,500 feet in the Chiricahuas, in Arizona; 7,200 feet in the Pinos Altos Mountains in New Mexico; and 8,000 feet near Coyotes, Durango, Mexico.

As to the Tamaulipan subspecies (*C. l. morulus*), I have been advised by Paul S. Martin that at least two of the type series came from the humid east slope of the Sierra de Guatemala, Tamaulipas, Mexico, at an altitude of about 5,300 feet. They were found in a relatively level pocket on a rocky mountain trail from Gómez Farías to La Joya. Here there were large pines, oaks, a few sweet gums, and firs. The pocket was surrounded by steep, rocky ridges, with scattered pines and a wealth of low agaves. Another was found in the corral of a cattle ranch, also a level place in a rocky area. A fourth specimen may have been taken on the arid western slope of the mountains. It is now known that the subspecies has an altitudinal range of at least 3,900 to 6,200 feet.

*Speckled Rattlesnake* (*C. mitchelli*).—The speckled rattlesnake is primarily a rock-inhabiting species, this being true of all four subspecies—the San Lucan speckled rattler (*C. m. mitchelli*) of central and southern Baja California; the southwestern speckled rattler (*C. m. pyrrhus*) of southern California, western Arizona, northern Baja California, and extreme northwestern Sonora; the Panamint rattler (*C. m. stephensi*) of east-central California; and the dwarfed form (*C. m. muertensis*) of rocky El Muerto Island. Throughout its range, it may stray for short distances onto desert flats or sandy washes, and in coastal southern California the subspecies *pyrrhus* frequents chaparral or cactus; but, generally speaking, wherever it is found, boulders, rock piles, or cliffs will not be far away. Although occurring in the coastal and the inland valley and mesa subzones of San Diego County, it is rare there, compared with its greater prevalence in the rocky foothills of both the western and eastern slopes of the mountains. The occasional strays along the coast are presumed to have been carried down by river floods.

Two other kinds of rattlesnakes, the southern Pacific and red diamond, are about as common in the coastal and mesa areas as they are farther back in the foothills; and, as their food requirements are the same as those of the speckled rattlers, there must be some other reason why the latter can compete with them in the foothills but has failed to become established along the coast. Possibly it is the lack of rocks, the speckled rattlers requiring rock crevices for refuges, whereas the others utilize dense shrubs, cacti, or mammal holes. But more probably it is a question of atmospheric humidity, especially fogs, for most of the range of *pyrrhus* is more xeric than those of *helleri* and *ruber*. The difficulty is not rainfall, since the annual precipitation in the cismontane foothills, which *pyrrhus* shares with the other two, is about double that experienced along the coast, where only an occasional stray is to be found.

In the Mojave, Colorado, and Sonoran deserts, one finds scattered mountain peaks and ranges rising above the surrounding plains. In the flatlands and on the great alluvial fans, the characteristic rattlers are the sidewinder (*C. cerastes*), the western diamond (*C. atrox*), and the Mojave rattler (*C. s. scutulatus*). By no means are all three found everywhere; each has its characteristic niche, although territories where any two occur together are quite extensive. But as soon as the base of a mountain is reached, with its tumbled boulders or rocky canyons, there some form of the speckled rattler is likely to be met. Often the species that prefer the flats will be found far up the sandy washes, thus overlapping the range of the speckled rattler.

I should not wish to convey the idea that the subspecies of *mitchelli* are addicted to barren boulders exclusively, for within their rocky habitats they often seek the shade of bushes just as do the other rattlesnakes. Both *stephensi* and *pyrrhus* have been observed issuing from mammal holes at dusk, so this kind of refuge is not shunned. A. Pierce Artran reports having found a southwestern speckled rattler in a rat's nest in Arizona. But more often they have been discovered concealed under rocks or in crevices. On at least two occasions, I have found the southwestern speckled rattler (*pyrrhus*) lying, as if by design, in front of a horizontal crevice in which it took refuge upon my approach. Johnson, Bryant, and Miller (1948, p. 275), in the Providence Mountains of the Mojave Desert, found *pyrrhus* in rocky outcrops, talus, and deep canyons along the base of the range.

The subspecies *C. m. muertensis* occurs only on the rocky islet of El Muerto of the San Luis group, in the Gulf of California. Dr. Charles H. Lowe, Jr., the collector of the type series, reported that all nine specimens were within 20 feet or less of safe retreats in rocky crevices or holes. The intense daytime heat and lack of shading vegetation made it imperative that they be near readily accessible shelters from the sun. I was advised by Nelson K. Carpenter, an ornithologist, that at dusk the little rattlers come down to the beach, where they are found among the drift just above the tide line.

As to altitudes, the subspecies *C. m. pyrrhus* is occasionally found up to 5,000 feet or somewhat above; for example: About 5,600 feet at Canyon Prieto near Prescott, Yavapai County, Arizona; 5,300 feet at El Piñon, San Pedro Mártir Mountains, Baja California; 5,000 feet near Keys View and also between Idyllwild and Keen Camp, Riverside County; and 5,500 feet in the Providence Mountains, San Bernardino County, California.

The Panamint rattler (*C. m. stephensi*) occurs still higher in the rocky canyons on the east slope of the Sierra Nevada, where it has been taken at 7,000 feet on Bishop Creek, Inyo County. This subspecies shows a strong addiction to arid, rock-strewn places.

*Black-Tailed Rattlesnake (C. molossus)*

I took a northern blacktail (*C. m. molossus*) in some vegetation among rocks about 100 feet from the stream in the Graham Mountains, Arizona. On Post Creek, a very large blacktail was taken right at the water's edge on a flat rock. This was almost at the edge of the canyon where it opens into the valley—just a few hundred yards from the end of the steep mountain sides and the beginning of the valley. The blacktail seems to be the most prevalent rattler in this range, and all the rattlers apparently live near the streams. *O. N. Arrington, Phoenix, Ariz.*



One black-tailed rattler in Ward Canyon, Chiricahua Mountains, was found coiled in an open area, but near rocks and brush. Another was taken in Rock Creek Canyon under a log. Still another *molossus* was collected in lower East Turkey Creek Canyon in a chaparral area near some brush. *Lawrence H. Cook, San Diego, Calif.*



Collecting in the Huachuca Mountains, Carlton Perkins and I found four black-tailed rattlers between July 21 and 25. The conditions were as follows: The first was sunning itself on a brown patch of grass at the top of a gorge. It rattled and swiftly took refuge under a rock. This was at 9 A.M., air temperature 90° F. The second was coiled at the entrance to a hole under a boulder, into which it immediately retreated upon seeing us. We required two hours to move the boulder, and then it went farther in under roots and rocks, so that it took another half hour to catch the snake, which had been first located at 10 A.M., 90° F. A couple of days later we got the other two. We found a cast skin beside a boulder and upon raising it found the snake beneath; this was at 10 A.M., 75° F., 6,000 feet. The last rattler was found with its head under a rock, as if trying to hide; 2 P.M., 75° F., 6,500 feet. In Montosa Canyon in the Santa Rita Mountains we got three, one crawling up a rocky trail in a wash at 6:15 P.M., one under a boulder near camp at 9 A.M., and one behind a rat's nest in a sort of cave in a bank at 2 P.M. *A. Pierce Artran, Los Angeles, Calif.*



I have collected rattlesnakes in southeastern New Mexico, in or near Carlsbad Caverns National Park, some of which were blacktails. In that area there are numerous small limestone caves and crevices in the rock strata which the snakes frequent, and it is usually rather risky to enter such places without carefully examining them. *Harold J. Brodrick, National Park Service, Yellowstone Park, Wyo.*

Although in Arizona the blacktail is largely a mountain, or at least an Upper Sonoran, form, preferring tree-shaded stony canyons, it is occasionally found in the Lower Sonoran zone, particularly in rocky foothills. A. E. Ball told me of finding it even out in the broad valleys and plains of Cochise County, Arizona. Ortenburger and Ortenburger (1926, p. 119) state that the blacktail prefers rocky canyons. Mosauer (1932d, p. 17) refers to its habitat in rocky, wooded canyons. MacCoy (1932, p. 24) found one on driftwood and twigs of bushes, four inches above ground. Another was found lying on twigs, leaves, and sand by the side of a large rock near a heavy cover of bushes. Humphrey (1936, p. 329) reports *molossus* at altitudes of 4,200 to 4,800 feet in tree-shaded canyons. Gloyd (1937, p. 128), in the Huachucas, found them in rocky slopes with loose stones, at the edges of rock slides, on ledges below trails, and one on a pile of boards in a shed. L. T. Murray (1939, p. 13) states that in the Chisos Mountains, Texas, the blacktail is usually found above 4,000 feet, in wooded and grassy locations.

Milstead, Mecham, and McClintock (1950, p. 544), in Terrell County, Texas, encountered blacktails in the persimmon-shin-oak association among rimrock and outcropping limestone. Woodin (1953, p. 295) collected *molossus* at 2,500 feet in the Tucson Mountains of Arizona, and at 5,300 to 7,000 feet in the Huachucas. He had a report of one found at the very top of Miller peak (9,440 feet). It has been reported as high as 9,000 feet in the Chiricahua Mountains of Arizona. Gloyd (1937, p. 128) obtained *molossus* at elevations varying from 5,200 to 8,000 feet in the Huachucas.

I am informed that the Mexican black-tailed rattlesnake (*C. m. nigrescens*) is also a mountain dweller, addicted particularly to rocky situations. It has been recorded as high as 8,000 feet near Coyotes, Durango, and at the same altitude in the Patzcuaro Basin, Michoacán. The Nelson-Goldman expeditions collected a number of specimens at altitudes of from 7,200 to 8,500 feet. The upper levels were in the Transition Zone, with abundant vegetation. Leopold (1950, p. 510) assigns most of the area occupied by *nigrescens* to the temperate pine-oak forest. It is probable that some southern blacktails are found in mesquite grassland, just as the northern subspecies is sometimes found in the arid valleys between mountain ranges.

*Mexican Lance-Headed Rattlesnake* (*C. polystictus*).—Paul D. R. Ruthling told me of collecting rattlesnakes of this species in the tules of Lake Chapala, Jalisco, Mexico. They were quite plentiful in tule stands above the water, and took refuge in the water when annoyed. About 20 to 25 were seen. This was on August 21, 1919. But by no means all of the rattlesnakes of this species that have been collected were found in such aquatic situations. Of one place, Plateado, Zacatecas, where Goldman collected *polystictus*, he says (1951, p. 288):

Specimens taken at 7,600 feet near the town and at altitudes up to 8,500 feet in the nearby Sierra Moroni were all labeled "Plateado." The rolling plains near Plateado are mainly open and grass-covered. The slopes of the Sierra Moroni above about 7,600 feet are covered with oaks, and pines grow along the crest of the range. Upper Sonoran Zone.

Specimens of *polystictus* whose altitudes can be determined would indicate an altitudinal range of from 4,800 to 8,000 feet, mostly in the temperate pine-oak forest of Leopold (1950, p. 510).

*Twin-Spotted Rattlesnake* (*C. pricei*).—The Arizona subspecies (*C. p. pricei*) is quite common in the Chiricahua Mountains of southeastern Arizona, and somewhat less so in the Pinalenos, Dos Cabezas, Santa Ritas, and Huachucas. Peculiarly enough, it dominates in numbers its competitor, the banded rock rattler (*C. l. klauberi*), in the Chiricahuas, whereas the situation is reversed, with the latter the more plentiful, in the Huachucas. This species is not found in the plains between the mountain peaks; the several montane populations are isolated from each other.

Lawrence H. Cook collected about 30 specimens of this subspecies for the San Diego Society of Natural History in the Chiricahuas in 1931, and reported as follows:

Two specimens of *pricei* were found in Barfoot Park on the 17th and 18th of June. Another was taken on the Crest trail near Rustler Park on the 28th of June. Live specimens were

taken in Long Park, head of Rock Creek Canyon (9,000 feet), Rock Creek Canyon (7,500 feet), and Ward Canyon. One was found in each of the first two localities, but the largest number came from Ward Canyon. One in Long Park was found in a grassy area, and at the head of Rock Creek Canyon on a small ledge of a large boulder. Those in Rock Creek Canyon were from a slope with shrubs, rocks, grass, and agaves. In Ward Canyon they seemed to occur in all situations, for I found them in or near rock slides, near grassy tree-studded areas, in brush, and in the open.



I collected a twin-spotted rattler in the Pinaleno or Graham Mountains at about 7,000 feet. It was 15 feet from a stream in a pile of rocks with sparsely growing vegetation and debris. O. N. Arrington, Phoenix, Ariz.

Gloyd (1937, p. 131) collected four specimens in the Chiricahuas at 7,200 feet. He found one coiled in sunlight on a ledge, another in a bunch of grass, a third coiled on a horizontal flat stone at the edge of a rock slide, and the fourth near the crest of the ridge in a shallow crevice among ferns, mosses, and lichens. The character of the country in the Huachucas and Chiricahuas where *klauberi* and *pricei* are found is discussed by Gloyd (pp. 84–88). Woodin (1953, p. 295) collected *pricei* in the Huachucas at 7,000 feet. One was taken on a rainy afternoon, lying in the open near a creek.

In Mexico most of the area inhabited by *pricei* is considered by Leopold (1950, p. 510) to be in the temperate pine-oak association. This has been verified by several field collectors. The maximum elevations from which *pricei* has been reported are 9,000 feet in the Chiricahuas and 8,900 feet in the Pinalenos, in Arizona; and 8,400 feet at La Unión, Chihuahua, and 8,500 feet near Las Adjuntas, Durango, Mexico.

The Miquihuanan subspecies (*C. p. miquihuanus*) is found in the temperate pine-oak association of southern Nuevo León and southwestern Tamaulipas, Mexico.

*Tancitaran Dusky Rattlesnake* (*C. pusillus*).—This little rattlesnake is found at moderate altitudes, usually above 5,000 feet, in Jalisco and Michoacán, Mexico. Gadow (1908, p. 513) found one in a fallen, decaying tree trunk. Dr. F. A. Shannon has advised me of the terrain where they occur on Cerro Tancitaro, Michoacán. This peak reaches an altitude of 12,660 feet. The little rattlers were most plentiful at about 6,000 feet, where there was a pine forest mixed with oaks, and with volcanic rock scattered about. The snakes were not in the pure pine forest, but were most often near the rocks.

*Red Diamond Rattlesnake* (*C. r. ruber*).—Ecologically speaking, this snake has a fairly wide tolerance. Although it occurs only in the Californias, it occupies areas quite diverse in character, where the rainfall ranges from about 3 to 30 inches per annum, and the vegetation is correspondingly variable. For example, in San Diego County it is found from the cool ocean shore, through warm inland valleys and mesas, to foothills covered with dense chaparral. It avoids the mountains above about 4,000 feet, but recurs on the easterly slope, which is much more rocky and barren, and continues its range well out onto the floor of the desert. The most easterly records are 3 miles west of Bensons Dry Lake in San Diego County, and 3 miles west of Plaster City, Imperial County. It is of interest to note that both of these records overlap the range of the most typical of desert rattle-

snakes, the sidewinder, by 15 miles or more. In Baja California *ruber* is found extensively in arid areas. At its northerly limit in California, it has crossed the San Gorgonio Pass and has become established in the Morongo Valley. However, it barely reaches into San Bernardino County, although widely prevalent in western Riverside County.

As to local niches, although brush-shrouded granite boulders and cactus patches are favorite lying-out places, this snake is by no means restricted to them. I have found it in grassy fields, orchards, amid brush of all kinds, beneath the bare rocks of the lower desert slopes, and in sandy desert washes. But in ranging about, it seems to prefer heavy brush. The following table indicates the relative frequency of roadside conditions where *ruber* has been found alive or run over:

Pond, creek, or river bank . . . . .	3
Cultivated field . . . . .	3
Grass . . . . .	4
Light brush . . . . .	3
Heavy brush, chaparral . . . . .	30
Trees . . . . .	2
Rocks, boulders . . . . .	14
Brushy desert . . . . .	9
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Louis P. Faldborg of Chula Vista has thus described his experiences in collecting the red diamond rattler in San Diego County:

Conditions under which rattlesnakes are found vary somewhat with altitude and season of the year. On the west and south slopes of Soledad, San Miguel, and Black mountains, red diamond rattlesnakes are readily found during the fall, winter, and early spring months, and especially on warm days preceding rains. These snakes are generally found in a coiled position, in sheltered caves of rock, at the mouth of a rock crevice or hole, just far enough out to allow the sun to strike them. I have reason to believe they crawl out during the day and back again at night, for on several occasions I have found them in the act of coming out about noontime. As spring advances and the hot dry days of summer come, the snakes on these slopes become far less numerous. If found at all they are in a stretched-out position or crawling through the brush.

On the lower lands, between the foothills and the ocean, these red rattlers are rarely found during the winter months. However, beginning in February and during the spring months until June, they are readily found in the warm, sunshiny ravines, with slopes facing the south that have an abundance of cacti, sumac, and brush, and are protected from the west winds.

On these lower levels, between foothills and ocean, beginning in June and during the summer and early fall months, a change in the activity of these red rattlers is noticed. They are then not alone confined to any place or condition as in the springtime. As a matter of fact, they are apt to be found any place. They seem then to be possessed of a roving nature. I have found them crawling in the open and the brush as well, at all times of the day from daylight till dark. I have also found them coiled and resting at all times of the day; and have found many instances suggesting that they travel a good deal at night during the summer months. At this time of the year I rarely find them in pairs or close together. The cactus is a favorite place for finding them, and I do not remember ever finding a snake on these lower levels that was not in a cactus clump, or within a few feet of one.

The San Lucan diamond rattlesnake (*C. r. lucasensis*), a subspecies of *ruber*, lives under somewhat similar conditions in southern Baja California. It is most

prevalent amid heavy brush and rocks about the Cape, but is also found in the desert east of Magdalena Bay, and in other arid sections in the southerly third of the peninsula.

*Mojave Rattlesnake* (*C. s. scutulatus*).—In California the Mojave rattlesnake is exclusively a desert snake. These greenish rattlers are found in many types of terrain, but are probably most common in level areas having a light brush cover, such as that between Mojave and Barstow. In this area they are almost entirely nocturnal, so that when they are caught the exact nature of the surroundings in which they are found must be ascertained by revisits in daylight. I have found them in rather barren wastes but not in the playas themselves, in grass, light brush, and heavy brush, amid yuccas and cacti, and, higher, in the Joshua-tree forests. They are not absent from rocky areas, but seem to have no particular need of rocks, and in most rocky sections are likely to be supplanted by one of the subspecies of *C. mitchelli*, either the southwestern speckled rattler (*C. m. pyrrhus*) or the Panamint rattler (*C. m. stephensi*). Johnson, Bryant, and Miller (1948, p. 275) found *scutulatus* in gently sloping alluvial fans, where the soil was coarse, rather firmly packed, and cut by shallow washes. This was near the Providence Mountains of San Bernardino County.

In Arizona the Mojave rattler is found in the same surroundings as the western diamond (*C. atrox*), a competitor that is absent from most of the California range of *scutulatus*. The Mojave is common in the brush-covered plains south and northeast of Kingman, and between Salome and Wickenburg. North of Wickenburg, in a country of grassy plains, creosote-bush mesas, watercourses fringed with mesquite, and rocky hills, it is quite prevalent, probably more so than the western diamond. It is also found farther north than *atrox*, for it occurs in the rock- and tree-studded prairies north of Prescott, at least as far as Drake and northeast to Sedona. About Tucson *scutulatus* is moderately common among mesquite, creosote bush, and cacti. Here again it shows a preference for flat country, leaving the rocks to such species as the tiger and black-tailed rattlers. Lee W. Arnold, collecting near Tucson, took three specimens in mesquite, and one each in opuntia, cholla, and burroweed. Woodin (1950, p. 295) found *scutulatus* in southern Arizona at the bases of the mountains, and at elevations of not over 4,900 feet. A professional collector operating near Mohawk found most of his specimens in the early morning under the banks of dry washes. Whether the Mojave rattler hibernates in rocky areas I do not know. For many years it was confused with the prairie, western diamond, and other rattlers, so that some of the older reports are not trustworthy. In the southerly part of its range in Mexico, *C. s. scutulatus* occurs primarily in the botanic zones called by Leopold (1950, pp. 512, 513) the temperate mesquite-grassland and to a lesser extent in the desert.

The Mojave rattler has been taken up to 4,950 feet in the Providence Mountains, San Bernardino County, California; above 5,000 feet near Prescott, Arizona; and up to 6,800 feet in the Chiricahua Mountains of Arizona. In Mexico it is found still higher, for it has been collected at 7,700 feet on El Oro Mesa, near Santa Barbara, Chihuahua. But it is not exclusively a high-altitude snake, for it occurs at sea level in extreme northwestern Sonora.

The southern subspecies, the Huamantlan rattlesnake (*C. scutulatus salvini*),

apparently occurs only at high altitudes, that is, between 5,000 and 8,300 feet. The type locality, Huamantla, Tlaxcala, is described as being on a high interior plain (8,300 feet) in the Upper Sonoran Zone (Goldman, 1951, p. 268). Another place where *salvini* occurs near Tehuacán, Puebla, is reported as arid, but with a luxuriant growth of desert plants, including yuccas, palmettos, and giant cacti. Goldman (p. 237) assigns the area to the Lower Austral Zone. Leopold (1950, pp. 512, 513) refers to these as temperate pine-oak and mesquite-grassland associations.

*Long-Tailed Rattlesnake* (*C. stejnegeri*).—I was told by Langan W. Swent, who succeeded in having a collector get two specimens for me, that they were found on the border of a pine forest, at the upper edge of a canyon dissecting a plateau.

*Tiger Rattlesnake* (*C. tigris*).—This is another rock-inhabiting form, preferring rocky hillsides or canyons. For example, it has been found on A Mountain, a rocky hill near Tucson, and in Sabino Canyon. Humphrey (1936, p. 329) collected 7 specimens at altitudes varying from 2,800 to 4,800 feet, all in rough, rocky places. It also occurs in rocky, semidesert areas around Guaymas, Mexico. Compared with most mainland rattlesnakes whose ranges have been established with considerable accuracy, it has a quite restricted range, for it is found only in a relatively narrow north-and-south strip in Arizona and Sonora.

*Cross-Banded Mountain Rattlesnake* (*C. transversus*).—Little is known concerning this recently described rattler, for the first of the three known specimens was not reported until 1940. It occurs up to 10,000 feet southwest of Mexico City, in what Leopold (1950, p. 509) considers a temperate boreal forest area.

*Dusky Rattlesnake* (*C. triseriatus*).—The Mexican dusky rattlesnake is a mountain form, reaching higher elevations than are attained by any other species. Earlier in this chapter I have mentioned the altitudes at which it has been found. It often occurs in rocky areas, although not restricted thereto. Gadow (1908, p. 61) found it under pine trees on a carpet of asphodels and tussock grass at 12,500 feet on Mt. Orizaba. He states (p. 513) that this species is characteristic of moist Mexican mountains. Paul D. R. Ruthling came upon a specimen on Mt. Ajusco at about 13,000 feet among patches of snow where bunch grass grew profusely. Another was found under similar conditions on Orizaba at about 15,000 feet. In a letter Ruthling commented on the probability that this species is restricted to montane islands:

The peculiar thing about the two little *C. triseriatus*, is that, although collected in places possibly 250 miles apart, the habitats were very similar. For miles in between were arid desert or semidesert valleys that would hardly provide means of transition for the species. It would seem that there are isolated islands of these rattlers, separated by barriers of lower open country of a different nature.

Davis and Smith (1953, p. 141) found *triseriatus* a fairly common snake in rocky and grassy situations, especially near water. This was in Morelos. Owing to the high altitudes at which these little rattlers live, they are frequently found basking in the sun in the open on clear days; on cloudy or rainy days they usually seek seclusion.

Dr. F. A. Shannon, who with his associates collected a large series (34) of *C. t. triseriatus* on Cerro Tancitaro, Michoacán, has kindly advised me concerning the

surroundings where the little snakes were found. Most of the collecting was done between 5,500 and 10,600 feet; the mountain reaches an altitude of 12,660 feet. He wrote:

The rattlers were most common at an altitude of 6,000 feet, where the general vegetation was pine forest, with oak mixed in around the large extruding volcanic rocks, especially in clearings. They were almost never in the pure stands of pine forest, but were seen and taken around and beneath the big rocks. They would often escape beneath these rocks as they were fairly alert for rattlesnakes. One was found under a log, another in thick underbrush on a south-facing slope of a canyon, and a third on the edge of a pine and oak forest bordering a ravine. In several areas around Tancitaro, the volcanic rocks were so thick (pedregal) and so free of soil that they supported little vegetative cover except algae and mosses. While no rattlers were taken in these black rocks, they were quite abundant around the perimeter. This was in June and July. Specimens from well up the mountain were usually taken on granitic boulders, where they were sunning themselves. The surrounding vegetation was coarse grass and scrubby pines. The maximum elevation at which a rattler was found was 10,600 feet.

The northern subspecies (*C. t. aquilus*) is also said to be addicted to rocky places, but with grass and trees about. It is a mountain form, but does not reach the extreme altitudes attained by its southern relative. Most of the area that it occupies is assigned by Leopold (1950, p. 512) to the temperate mesquite-grassland association, although some rises to the pine-oak forest.

*Aruba Island Rattlesnake* (*C. unicolor*).—Aruba Island, off the coast of Venezuela, the only place where this rattlesnake occurs, is arid and dry, except during a short rainy season. It was said to have been heavily wooded in pre-Columbian days, but subsequently the trees were cut down for charcoal, and erosion has prevented reforestation.

*Western Rattlesnake* (*C. viridis*).—This species ranges over so wide a territory, with such divergent ecological characteristics, that the several subspecies will be discussed separately. I have already mentioned in this chapter the maximum altitudes at which some of the subspecies have been seen.

*Prairie Rattlesnake* (*C. v. viridis*).—This subspecies of the western rattlesnake is an inhabitant of the western prairies up to and including the foothills of the Rockies. It prefers the grassy plains, country with a light brush cover, or areas where sandstone outcrops and buttes are numerous. But, of all habitats, it is probably most at home in the grassy plains, the country of the prairie dog and the burrowing owl—or was, before the advent of the white settler.

Rattlers are located in the bluffs and rocky parts of the county. *C. C. Hendricks, Oberlin, Kans.*



Rattlesnakes prefer rocky places in this district. *H. D. Byrne, Concordia, Kans.*



Rattlers are discovered occasionally in the sand-hill area, and in the southeast along the Missouri River, especially in rock ledges bordering streams. They are not common in this state; too much of the land is cultivated. *M. Bardwell, Lincoln, Nebr.*



When away from their dens in the summertime, prairie rattlesnakes may be found in any sort of surroundings, in grasslands, or sagebrush types. *Glenn Flathers, U. S. Forest Service, Camp Crook, S. Dak.*

As for the kind of country in which prairie rattlesnakes range, I have seen them on the prairie, in foothills, and among the buttes. Their summer refuge is usually under slab-rocks in the buttes, and under lumber piles, or old debris, on the prairie. They often use an old gopher hole; or a pile of rocks is a good place to expect them. Rattlers seem to prefer a dry country; however, it is not unusual to find them along a small creek or stream. *Calvin A. Bowman, U. S. Forest Service, Deer Lodge, Mont.*



Prairie rattlesnakes prefer the rolling prairie country where there is a limestone formation. *William T. Sweet, Butte, Mont.*



Rattlesnakes are likely to be most active between sunrise and sunset. They seek the shade of shrubs, rocks, holes, trees, plants, etc., during clear hot days. They den for the most part in rock slides, small caves in rocks, and deep fissures in cliffs and escarpments. In summer they are usually found in grasslands, sagebrush, greasewood, scattered ponderosa pine lands, or barren ground. *B. A. Goodman, U. S. Forest Service, Stanford, Mont.*



Rattlesnakes are usually found around the badlands and rocky sandstone ledges below 6,000 feet elevation. *W. J. Petermann, U. S. Forest Service, Meeteetse, Wyo.*



In the summer I have found rattlers most plentiful around prairie-dog towns. *William Lakanen, Game Warden, Rawlins, Wyo.*



Rattlesnakes are most often found on dry hillsides and flats. It does not seem to matter much as to the type of cover; I have found them in heavy timber, in the brush, and on grassy or barren areas. *Norman R. Tripp, U. S. Forest Service, Slater, Colo.*



In the high country, rattlesnakes are more active during the day, when they will be found out in the open in the sun; they seem to prefer to stay among the rocks and bluffs at other times, probably because the rocks hold the heat for a considerable time after the sun goes down. *O. J. Olson, U. S. Forest Service, Buckhorn, N. Mex.*

In the Bitterroot Mountains at the southwestern corner of Montana, the prairie rattlesnakes filter through the mountain passes into the Lemhi Valley of Idaho. Farther westward down the Salmon River this subspecies intergrades with the northern Pacific rattlesnake (*C. v. oregonus*). In this western outpost, the prairie rattlers inhabit territories quite different from their accustomed prairies and grasslands of the upper Missouri basin.

Rattlesnakes in the Salmon Forest frequent the south exposures where it is warm and dry. They prefer such situations to areas having heavy timber stands. *T. V. Pearson, U. S. Forest Service, Salmon, Idaho.*



Rattlesnakes are likely to be encountered in any kind of terrain, open grass, sagebrush, rocky, etc., until summer temperatures prevail, at which time they are usually encountered in slide-rock stretches where ninebark, chokecherry, mahogany, and other shade-producing shrubs offer protection from the sun. *Irwin C. Robertson, U. S. Forest Service, Salmon, Idaho.*

Because the prairie rattlesnakes are so conspicuous at the dens, when entering in the fall or leaving in the spring, as compared with the infrequency with which they are encountered when dispersed over their summer range, most of the accounts of their ecology are affected by the character of the ground where the dens are located. Probably they seek the open grasslands more than is generally supposed, although necessarily influenced by the nature of the ground preferred by their rodent prey.

*Grand Canyon Rattlesnake* (*C. v. abyssus*).—This snake, as its name implies, is a resident of the vast rocky cliffs of the Grand Canyon. It is essentially a rock dweller. It has been taken from the bottom of the canyon up to an elevation of 7,000 feet on the Tanner Trail, and at Navajo Point; and at 7,550 feet at Dutton Point.

*Coronado Island Rattlesnake* (*C. v. caliginis*).—This stunted rattler occurs only on South Coronado Island, a rocky, fog-shrouded islet, with a brush and cactus cover, that lies off the coast of Baja California just south of the international boundary.

*Arizona Black Rattlesnake* (*C. v. cerberus*).—This rattlesnake is found in the high plateau area of central Arizona, where it occurs most frequently either in sparse forests or on brush-covered slopes, leaving the grassy plains to its near relative, the Arizona prairie rattlesnake (*C. v. nuntius*). In the southern part of the state, it is restricted to the mountains; there are isolated colonies in the Santa Catalina, Rincon, and Pinaleno mountains, which represent the southern limit of its territory. It is apparently absent from the thoroughly collected mountain ranges farther south—the Santa Ritas, Huachucas, and Chiricahuas.

Black rattlers seem to prefer the wooded areas at about 6,000 feet and above. *J. T. Wright, Tucson, Ariz.*



In collecting Arizona black rattlers, I have found them up to 8,000 feet, though they do not appear to be abundant much above 6,500 feet. During the dry fall and spring weather, they seem to remain in close proximity to running streams or lakes; but during the months of July and August I have found them in the pine timber a mile or so from the nearest water. During this period they move about considerably. It appears that they are active only in the late afternoon and early evening. The daytime hours are usually spent under the roots of an overturned tree, within a hollow stump, or in some other hiding place. *A. W. Mollison, U. S. Indian Service, McNary, Ariz.*

From my own experience, I know *cerberus* to occur in the sparse forest country west of Ash Fork, and farther westward in the juniper areas where the country is partly flat and partly rolling, with some rock outcrops, around Glead and Crookton. I should call this essentially a forest snake, although the forest need not be dense.

*Midget Faded Rattlesnake* (*C. v. decolor*).—This little rattlesnake seems to prefer rocky and arid areas, judged by its habitats in the upper Colorado River basin and the basin of the Green River, in Utah and Wyoming.

Rattlers are found most frequently in rocky ledges, where they enjoy the warmth absorbed by the rocks and the protection afforded from weather and enemies. *Earl C. Sanford, U. S. Forest Service, Vernal, Utah.*



It has always seemed rather peculiar to me that more rattlesnakes are not found in the vast area of rimrock, and juniper and piñon rough lands surrounding this forest, since lands of the same character in Routt County, situated 100 miles to the north, are the natural home of the rattlesnake. According to old-timers, however, rattlesnakes were never numerous in any portion of Mesa County. *Ray Peck, U. S. Forest Service, Grand Mesa, Colo.*



I have seen these little rattlers up to 8,000 feet in Escalante, Roubideau, and Tabeguache canyons. *H. F. Harlow, U. S. Forest Service, Delta, Colo.*

Other high points, all in Utah, where this subspecies is known to occur, are: Blue Mountain, 25 miles east of Vernal, Uintah County, at 8,000 feet; Pay Gulch, 6 miles northeast of Altonah, Duchesne County, at 7,300 feet; and near Kenilworth, Carbon County, at 7,000 feet.

*Southern Pacific Rattlesnake* (*C. v. helleri*).—This is the common mountain and coastal rattlesnake from Santa Barbara County, California, south to the San Pedro Mártir Mountains of Baja California, with scattered occurrences still farther south. It ranges from the sea coast to the mountain peaks, but becomes increasingly scarce as one descends the eastern or desert slope.

In San Diego County, where the terrain is quite variable, there is an opportunity to observe how catholic the southern Pacific rattlers are in their choice of habitats. They are likely to be found everywhere from the ocean shore, just beyond the wash of the waves, through valleys and foothills, and from the peaks of the highest mountains down to the desert slope. The only area untenanted is the desert itself. I have found them in open fields, in orchards and vineyards, along streams, in cactus clumps and heavy chaparral, in granite crevices or under boulders, in grass-covered mountain meadows or the ferns of the hillsides, and where the timber was densest. On the eastern slopes they have been collected in the rock-strewn foothills, or in mesquite patches in such places as Borrego Palm Canyon, Tubbs Spring, San Felipe Valley, La Puerta, and Mountain Spring. But much collecting has failed to disclose any in truly desert areas, although three other species of rattlesnakes—the red diamond, speckled, and sidewinder—are not uncommon there.

In traveling about, I have kept notes of the roadside surroundings where snakes have been found, either alive, or dead on the road (DOR is the notation generally used in statistical reports). The record for the southern Pacific rattler is as follows:

Orchard or vineyard . . . . .	4
Cultivated field . . . . .	12
Grass (uncultivated field) . . . . .	33
Light brush . . . . .	7
Heavy brush, chaparral . . . . .	19
Trees, forest . . . . .	9
Rocks, boulders . . . . .	7
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The kinds of refuges that southern Pacific rattlers seek in the daytime when they are not foraging, are indicated by the following list, showing where specimens have been found in San Diego County:

- A juvenile under a dead log
- Three medium-sized specimens under a single flat rock only about 15 inches in diameter
- Three in crevices in a pile of granite rocks
- One stretched out under a manzanita bush
- One stretched out among oak leaves
- One coiled in a depression in a path bordered by ferns
- Two in a crack in a large granite boulder in an oat field

On several occasions I have found rattlers of this and other subspecies lying in front of rock crevices, or before rocks with a hollow space below, as if consciously ready for escape, should danger threaten. The following are reports from my correspondents regarding rattlesnakes of this subspecies:

This is a brush-covered area and rattlesnakes have been found along the trails near water and away from water. The territory I travel in is the mountains of the Coast Range between Piru Creek, the upper Sespe, and the Matilija drainages, Ventura County. Rattlers are found in almost all of the brush-covered area. *E. M. Lyda, U. S. Forest Service, Ojai, Calif.*



On our hot summer days I have found rattlers under brush and bushes, lying in the shade of a fallen log, or under a rock. *K. R. Halstead, San Bernardino, Calif.*



In the mountain areas during the months from May to October, I saw more rattlers along the stream beds and washes, and adjacent to lake shores at elevations of 2,000 to 6,000 feet, than at any other locations. They seem also to like the medium cover of shrubs and rocks more than the heavier wooded locations. It is my belief that they stay around the water at times because of a better chance of getting food, such as small rodents like the chipmunks that come for water. *Walter F. Emerick, Division of Fish and Game, Palm-dale, Calif.*

*Great Basin Rattlesnake* (*C. v. lutosus*).—The Great Basin rattlesnake is a dweller in the arid plains and desert areas between the Rockies and the Sierra Nevada, and of the scattered mountain ranges that rise above the plains. While found in irrigated areas, it is less prevalent there than in the wilds, although Linsdale (1940, p. 251) reported it to be especially numerous around alfalfa fields.

Around Zion Park these rattlesnakes seem to be especially partial to scrub-oak sections where the brush is thin and the terrain rather rocky. This may possibly be due to the fact that such areas are the hiding places of many small rodents. *Russell K. Grater, Rocky Mountain National Park, Estes Park, Colo.*



I have seen rattlesnakes on the foothills and in the higher mountains throughout the belt occupied by big sagebrush (*Artemisia tridentata*) and Gambel oak (*Quercus gambeli*) from southern Idaho to central Utah. In the Idaho country, along the Snake River Valley from Burley, Idaho, west and north, I have seen rattlesnakes in the box canyons of the Snake River and its tributaries. They are common to abundant in the box canyons in the vicinity of Hagerman, Idaho. I have seldom seen them until the month of May in the Utah foothills along the Wasatch front, near Salt Lake City and Ogden, Utah. During August I have frequently seen them near the streams. They are annoying to fishermen at this season. *O. E. Winkler, Salina, Utah.*



Rattlers are fairly abundant in the Smith's Prairie country, especially where the south fork of Boise River Canyon borders the prairie. This is about 65 miles east of Boise, Idaho. This particular stretch of canyon is characterized by lava-rock cliffs or rimrock. It is in these rimrock areas that rattlers are found and it has seemed to me they prefer lava-flow areas in that section. *F. LeRoy Sprague, U. S. Forest Service, Atlanta, Idaho.*



As far as the summer range is concerned, rattlesnakes summer almost any place. I have killed them on the desert 10 miles from water many times, and in the mountains in shale rock and along creeks, too. *Albert Madarieta, Oakley, Idaho.*



An arid to semiarid habitat is preferred by the local rattlesnakes. In mountainous sections, they are usually associated with outcrops of rocks, such as talus slopes. *Ernest H. Taylor, U. S. Forest Service, Victor, Idaho.*

Most of the rattlesnakes are found in localities having a south, southwest, or west exposure, with a lava-rock cliff or slide formation. However, many of the snakes actually discovered are found in irrigated gardens or along the banks of irrigation ditches of the ranches within the above general localities. *N. D. Millard, U. S. Forest Service, Boise, Idaho.*



Occasionally rattlesnakes are found near the irrigation canals and laterals, but mostly they are in the northeasterly part of the county, which is arid. *George B. Haddock, Shoshone, Idaho.*



In north-central Nevada at altitudes of 6,000 feet, rattlesnakes do not travel far enough from their dens during the short summer to cover all the country, as they do in warmer climates, with long frost-free periods. They are abundant in some localities but there are none in others. *Phil Kennedy, U. S. Forest Service, Douglas, Ariz.*



Rattlesnakes are especially frequent in the vicinity of the rimrocks bordering the Pit River Valley and its tributaries, from Goose Lake to Big Valley. There are places where they are fairly numerous in the more recent lava flows near the western border of Modoc County. They are seldom found in the flat pine-woods areas away from the rocky sections. In fact, they do not seem to frequent the heavily timbered areas. *Ivan A. Cuff, U. S. Forest Service, Canby, Calif.*



One significant thing I have noticed about the rattlesnakes hereabouts is that their occurrence is spotty. For instance, at my south ranger station, they are very plentiful. There is a rocky slope with a south exposure across the creek from the house. We find many snakes around the house, even though they must cross ditches and streams to reach the area. *Glen R. Jones, U. S. Forest Service, Bridgeport, Calif.*

*Arizona Prairie Rattlesnake* (*C. v. nuntius*).—This little snake inhabits a more arid territory than its larger relative (*C. v. viridis*) of the eastern slope of the Rockies. In its most typical form it is found in the basin of the Little Colorado River, including the Painted Desert, especially between Holbrook and Canyon Diablo. This is a high mesa (4,800 feet and up), usually with red or red-brown soil, thin grass, and small bushes. Rock outcrops are frequent, and the water-courses are usually deeply cut, with clifflike banks. Although the Arizona prairie rattler dens in rock caves, in summer it ranges widely over the plains amid the sparse grass and low bushes. Here the speckled earless lizard (*Holbrookia maculata approximans*) abounds; it comprises a part of the food of the little rattler.

East of Navajo and west of Canyon Diablo the country is stonier, rougher, and more rolling. The vegetation is increasingly dense, and junipers abound. Here the snakes are larger and darker in color. This larger form also is found on the high plain between Williams and the Grand Canyon. This subspecies reaches considerable altitudes—6,900 feet at Flagstaff, 7,080 feet at Wildcat Hills, and about 7,000 feet in Medicine Valley, all in Coconino County, Arizona.

*Northern Pacific Rattlesnake* (*C. v. oreganus*).—The northern Pacific rattlesnake is one of the most broadly tolerant of all rattlers in its choice of habitats. It is found from the seashore to an elevation of at least 11,000 feet in the mountains, and alike in arid and humid territories. Latitudinally it is widely dispersed, ranging from Lat. 35° N. in California to 51° N. in British Columbia. It occurs in arid plains and fertile valleys, rolling grasslands, chaparral-covered foothills, on rocky ridges, and in mountain meadows and forests. It inhabits areas where the annual rainfall barely attains five inches and the Sierra Nevada, where the

snowfall is as great as in any part of the United States. Yet even with this catholic taste, one notes a selective trend toward an ecological mode. This is well illustrated by comparing the ranges of this snake in British Columbia and in south-central California. In the former it is restricted to the driest areas, for much of the province, especially the coastal region, is too moist. But in south-central California, a much more arid area, this rattler inhabits the most humid sections available, the coastal belt and the Sierra Nevada, rapidly declining in numbers in the desert foothills, and it is absent from the desert itself. Its absence in the desert is not owing to a lack of food, for other species of rattlers flourish there.

The following extracts from the letters I have received regarding the habitats of the northern Pacific rattlesnake will illustrate the many types of terrain in which it lives:

In British Columbia rattlesnakes are found only in the dry belt. *D. Cameron, Salmon Arm, B. C.*



Rattlesnakes are well distributed along the Salmon River and its side streams. The small ones mostly stay along the creek bottoms, ranging up the open, rocky sidehills for short distances. They are often found coiled near the edge of a stream during the middle of the day. *H. W. Higgins, U. S. Forest Service, Avery, Idaho.*



In the Bitterroot National Forest, at the head of Selway River and a portion of Salmon River, rattlesnakes were abundant, generally speaking, on the south and westerly exposures along the main rivers. On the Selway they did not occur more than 4 or 5 miles up any side stream and then only on the favorable exposures. On the Salmon River they range as high as 7 or 8 miles up the side streams from the main river, unless the elevation is too great. *George W. Case, U. S. Forest Service, Saint Maries, Idaho.*



Rattlesnakes are found to the west and north side of the Salmon River. This area is open, yellow-pine timber on steep slopes, bluffs, and rockslides. *Paul H. Strand, U. S. Forest Service, Dixie, Idaho.*



Rattlers prefer rocky, steep country with some vegetative cover for shade; and in the heat of summer prefer to be not too far from water. *F. E. Williams, U. S. Forest Service, Rig-  
gins, Idaho.*



Pacific rattlesnakes are very abundant along the northeast side of Lake Chelan on rocky, south exposures. They are fairly abundant on steep, rocky, southern exposures in the Methow, Okanogan, and Columbia valleys up to an altitude of about 4,000 feet. On the Methow River there are many rattlers on the northwest side, while on the southeast side there are almost none. They are not great travelers. *George R. Wright, U. S. Forest Service, Mazama, Wash.*



I have found many rattlers and 90 per cent were in bush grass or succulent brush where one would expect to find mice and other small creatures. They seem most numerous along streams. I've seldom seen any out among the rocks or on dry soil of semiarid country. *C. K. Lyman, Newport, Wash.*



Rattlesnakes in this county are found in the lowlands as well as in timber. *Norman Min-  
nick, Ontario, Oreg.*



Rattlesnakes go long distances from their winter dens and are often found in grain shocks and hay bunches, as they can hide there, and also mice are to be found for food. *Lawrence  
Kelly, Harper, Oreg.*

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The kind of surroundings and country rattlers prefer depends on the time of year. Mostly they have their dens in rock crevices, where it warms up the quickest in springtime. These are generally on south exposures and cliffs. In the heat of summer they will be found near the coolest places that afford protection from the heat, and also where there is more food. Close to streams is a good place to look for them during the hot season. They are found at different altitudes, but it depends on the climate as to the elevations they reach. In timbered country they don't generally get above 3,600 feet. *W. D. Royster, U. S. Forest Service, Paulina, Oreg.*



Though we find rattlesnakes at a rather high elevation, for a country which is not far removed from the coast, they are generally in open pine timber and areas of rock outcroppings. They are not found in areas of dense timber, such as the fir forests on north hillsides. Ordinarily there are more snakes found in the lower elevations than higher up. *L. J. Cooper, U. S. Forest Service, Merlin, Oreg.*



The range of the rattlesnakes in the Rogue and Illinois watersheds does not, except in rare cases, extend more than a mile back from the rivers. *F. K. Lightfoot, U. S. Forest Service, Agness, Oreg.*



I have found rattlers in heavy-shaded timber areas as well as in dense brush. But they are definitely more numerous in rocky exposed places with lighter cover. *Harvey E. Zink, U. S. Forest Service, Sawyers Bar, Calif.*



In this part of the state, rattlesnakes are most numerous in the foothill areas. They prefer a brush- or timber-covered, or rocky terrain. Loose shale or lava cliffs seem most likely to be selected as dens. *Victor R. Hake, U. S. Forest Service, Berry Creek, Calif.*



Rattlesnakes favor regions which are fairly hot, brushy, and rocky. I have found them in the pine forests, but have seen more in rocky canyon slopes along small water courses. *J. T. Kenney, U. S. Forest Service, Dardanelle, Calif.*

That northern Pacific rattlesnakes are often found along water courses in summer has been mentioned in several of the comments already given. Others to the same effect follow:

Most of the rattlesnakes I have gotten (averaging 20 per year) have been those crossing the roads or in the vicinity of streams. *D. D. McLean, Division of Fish and Game, San Francisco, Calif.*



Rattlesnakes are distributed fairly well over this area, but are found mostly along the water courses. *John L. Monday, U. S. Forest Service, Covelo, Calif.*



Rattlesnakes are often killed along the county road in the evening, apparently going to the river for water. *Earl Leitritz, Copco, Calif.*

John P. Dern made the following habitat and other notes on northern Pacific rattlers met on a pack trip into the Kings River section of the southern Sierra Nevada of California in 1939:

June 21: Between North Fork, Kings River, and Rancheria Creek: Killed a large rattlesnake which gave us ample warning as we approached. We found him in the shade of a yellow pine, entwined in green moss on a granite rock. 10 A.M., 80° F., 6,400 feet.

June 24: On Middle Fork, Kings River, between Tehipite Dome and Simpson Meadow, north bank: Killed one rattlesnake this morning. He gave us good warning. He was located by the side of a granite rock under a fern in semidry habitat. 11:20 A.M., 75° F., 6,100 feet.

June 25: On Middle Fork, north of its junction with Cartridge Creek: Killed our third

rattlesnake at 11:15 A.M., 80° F., 6,700 feet. Both my companions had passed him before he sounded off with his rattles. He was about five feet off the trail on a granite rock.

June 30: Returning, on the north bank of Middle Fork, going down stream from a point two miles below Goddard Creek: During the morning we encountered rattlesnakes at frequent intervals, six in fact. Practically all were encountered in short grassland—with grass four inches high at the most. This grassland was level to gently sloping. All six snakes appeared to be headed from granite stones above, toward the river below, a distance of from 40 to 150 feet. Few of them gave us any warning, and none emitted a sound until one of us had spotted it first. The altitudes ranged from 5,000 to 6,700 feet; air temperature about 80° F.

Besides the desert, and the highest mountains above 11,000 feet, which I have discussed separately under altitudes, there is one other area in which the northern Pacific rattlesnake—or any other rattler, for that matter—has been unable to maintain itself. This is the coastal redwood belt of the northwestern California coast, and similar coastal areas in Oregon and Washington. Not only are rattlers found close to these areas, but they are occasionally carried in by floods, yet they seem never to secure a permanent foothold. It is doubtful that a lack of food can be controlling, since various small mammals of a size suitable to rattlers are plentiful in these sections. Probably the excessive and almost continuous wetting in the form of fog or rain is the controlling factor; although the temperature is notably low in summer, other snakes, including the ovoviviparous garter snakes, have no difficulty in bringing their young to term.

The following are remarks from my correspondents on this situation:

The nearest to the coast I have ever killed a rattler was about five miles in a straight line. *Leo A. Mitchell, Point Arena, Calif.*



Rattlesnakes infest this district to some extent, but are very seldom found in the redwood belt. *Earl Macklin, Game Warden, Ukiah, Calif.*



Rattlers are fairly common in the hill country here, especially where there are rocky sections, with more or less open land roundabout. But they are almost unheard of in the redwoods, where we live. One was reported killed on an old road in the hills just on the edge of the redwoods, between here and Bridgeville, many years ago, and another on the school grounds of Bridgeville.

It has been reported that a rattlesnake has occasionally been found in the Eel River Flats, but never living there, just washed down from the interior regions during winter floods, when trees and other wreckage have come down. *Charlotte M. Wilder, Carlotta, Calif.*



Generally, it is our observation that rattlesnakes are not found in the heavy timber types adjacent to the coast, or in the larger, northerly river bottoms where there are stands of Douglas fir; however, as one goes inland in the Umpqua, Rogue, and Willamette river drainages they are found in increasing numbers. *G. E. Mitchell, U. S. Forest Service, Grants Pass, Oreg.*



There are no rattlesnakes in the heavy timber and none on the west coast. But there is an exception to every rule, and a very interesting case occurs in Cowlitz County on the north bank of the Columbia in Washington, hardly 40 miles from the Pacific Ocean. This is a monadnock peninsula of columnar basalt projecting into the river. The upstream side is a driftwood trap, and from this drift, which has run the Cascade Rapids, there has been released a lively colony of rattlesnakes that have found the warm creviced rock very much to their liking, and there they are a menace to the quarrymen. *Richard J. Grace, Portland, Oreg.*

The Lake Tahoe area is another that, although completely surrounded by sections in which rattlers are common, has few if any itself.

Although rattlesnakes abound in the territory surrounding the Lake Tahoe Basin, they are rare or absent within, for they do not come over the mountain rim. Possibly our period of low temperatures is too long (September to June). The only instance of which I have heard of rattlesnakes killed within the basin, was of two about two miles west of Lake Tahoe, elevation 6,700 feet, in 1935. J. C. Lewis, *Tahoe Fish Hatchery, Tahoe, Calif.*

Fitch (1949a, p. 514), who made a most complete study of the natural history of the northern Pacific rattlesnake, as found on the San Joaquin Experimental Range, in Madera County, California, says they occupy a woodland belt in a rolling terrain, with some open grassland, with frequent granite outcrops, often in extensive piles. The flora predominantly comprises annual forbs and grasses.

Hawken (1951, p. 81) has pointed out how sharply the range line of *oreganus* may be drawn in a territory showing no conspicuous ecological variations. In one place, a natural trap yielded 492 snakes in a single year, without a rattler among them. A short distance to the south rattlers were quite common. This was in the coastal mountains of San Mateo County, California.

The most arid area occupied by *oreganus* is the west side of the San Joaquin Valley, an area of rolling, almost barren hills. Here it is not merely an edge invader, as it is on the southeastern slope of the Tehachapis where these mountains descend into the Mojave Desert, for the western San Joaquin is in the center of a large area occupied by *oreganus*. These west-side snakes are lighter in color than the subspecies is elsewhere; superficially they resemble the Great Basin rattler (*C. v. lutosus*).

*Ridge-Nosed Rattlesnake (C. willardi).*—This is another mountain rattlesnake like *pricei* and *klauberi*. The northern subspecies (*C. w. willardi*) is found, but is not common, in the rocky canyons of the Huachuca Mountains of southern Arizona, up to 8,000 feet. In northern Sonora, Mexico, it has been collected in the Sierra de Ajo, on Cerro Azul, and in the Sierra Aconchi, in what Lowe and Marshall describe as a pine-oak association. Woodin (1953, p. 295) found one under a log in the Huachucas at 7,500 feet, and another under a board at 6,200 feet. A. E. Ball informed me that he found specimens among gray rocks in an open forest. These rocks were not part of a rockslide, but were imbedded in the soil and some were moss-covered. In the Santa Rita Mountains, the only other range besides the Huachucas wherein *willardi* occurs in the United States, it has been found up to 9,000 feet. It is doubted that *willardi* occurs below the wooded sections of these mountains, that is, below 5,000 feet.

The Chihuahuan subspecies of the ridge-nosed rattler (*C. w. silus*) is found in the mountainous area of western Chihuahua and northeastern Sonora. It occurs at altitudes of 5,500 to 8,000 feet, in places characterized by rocky canyons with dense underbrush, as well as mountain slopes with pines and oaks, and some open parks and grasslands. Lowe and Marshall (*in litt.*) consider it primarily a resident of the pine-oak forest. The southerly subspecies (*C. w. meridionalis*), like the other ridge-nosed rattlers, is a mountain form living at altitudes up to 8,000 feet in southwestern Durango and western Zacatecas.

*Massasauga* (*Sistrurus catenatus*).—The eastern massasauga (*S. c. catenatus*) lives largely in swamps, into which it may have been driven by the cultivation of the prairies where once it made its home. But as early as 1849, Warburton (vol. 1, p. 175) had already remarked on the addiction of massasaugas to swamps, so it may be that damp areas have always been their preferred habitation, although Hay (1892, p. 535) thought that cultivation of the prairies (rather than destruction by hogs, as some supposed) had diminished the numbers of massasaugas, and driven the remnants into the swamps.

Whatever the cause, there is now little doubt that the massasauga is largely restricted to swampy and primitive areas, as the following territorial reports will indicate: *New York*—neighborhood of swamps although shunning actually wet places, in moss, among bushes, or under evergreen trees, in hayfields at harvest season (Wiffen, 1913, p. 949); *Pennsylvania*—in the swamps in the western part of the state, where they take refuge in hummocks, in summer moving out to fence rows, under debris, or in hayfields bordering the swamps, but avoiding forests (Atkinson and Netting, 1927, p. 40; Netting, 1932, p. 10; Swanson, 1952, p. 179); *Ontario*—swamps, but also some in dry, rocky situations (LeRay, 1930, p. 201); *Ohio*—swamps and grassy meadows, grain shocks in summer, increasingly scarce because of swamp drainage (Morse, 1904, p. 137; Conant, 1938, p. 115; 1951, p. 255); *Michigan*—swamps, several being found in high dry clumps of grass within the swamps (Notestein, 1905, p. 121; Roberts and Quarters, 1947, p. 6); *Indiana*—prefer low wet ground, but are not aquatic (Hay, 1892, p. 535; Allyn, 1948, p. 13; Minton, 1950, p. 318); *Illinois*—bogs, swamps, and moist prairie, but avoid standing water (Wright, 1941, p. 659; Lueth, 1941b, p. 20); *Wisconsin*—swamps (Pope, 1925a, p. 14); *Minnesota*—swampy bottomlands (Breckenridge, 1944, p. 152); *Iowa*—having been driven out of fields by cultivation, they now remain only in the swamps (Guthrie, 1926, p. 187), although Loomis (1948, p. 122) found two in a semicultivated valley; *Missouri*—a lowland form, typical of the prairie and the plains in the west and swampy woodlands in the east (Evans and Gloyd, 1948, p. 230); *Kansas*—low sandy places near rivers and small streams (Branson, 1904, p. 423); or, swampy places, except in summer when they move into drier situations (H. M. Smith, 1950, p. 298).

Certainly these comments are almost in complete agreement that the eastern massasauga is essentially an inhabitant of swamps and bogs, but there is evidence, as stated by Wright (1941, p. 659), that they were once abundant in the prairies. K. P. Schmidt has advised me that they are still to be found in dry woods and rolling country in the Cook County (Illinois) Forest Reserve, where primitive conditions have been maintained.

The western massasauga (*S. c. tergeminus*), living in less intensively cultivated areas, seems still to be a dweller in open fields and grasslands. Strecker (1910, p. 16) reported the killing of some 25 to 30 in one wheat field in Texas, when the shocks were being moved. In Missouri, it is found in the prairie and plains of the northwestern corner of the state (Evans and Gloyd, 1948, p. 230). It has been observed as high as 6,000 feet near Vaughn, New Mexico.

*Pigmy Rattlesnake* (*Sistrurus miliarius*).—The various subspecies of the pigmy rattlesnake are found in the lower Mississippi Valley, the Gulf coast, penin-

sular Florida, and the coastal areas of the southeastern states. It is essentially a lowland form. Carr (1940, pp. 12-24, 95) reported the Florida subspecies (*S. m. barbouri*) as having a preference for wire-grass flatwoods; other habitat associations were stated to be limestone flatwoods, upland and tropical hammocks, flatwood ponds, freshwater and salt marshes, bayheads, and lakes. When the Everglades are flooded, pigmy rattlers are to be seen in small trees, or coiled on cabbage-palm leaves 8 to 10 feet high. Several were found under logs on the shore of Lake Yale.

Allen and Neill (1950b, p. 10) say that pigmy rattlers in Florida occur most often in palmetto flatwoods, or areas of slash pine or wire grass—in fact, anywhere near lakes, ponds, or marshes. Neill (1952, p. 48) found them abundant about the borders of cypress ponds in flatwoods. Herbert Kulp of Niceville, Florida, wrote me that he had found them under logs, and beneath turpentine cups that were set close to the ground. In Mississippi, Allen (1932, p. 18) found pigmy rattlers in winter under logs in the drier sections of swamps. In summer they were in the vicinity of lowland streams and dense thickets. Fannye Cook (1943, p. 50) reported them as being most often located beside logs or in trash. In Louisiana, Fitch (1949b, p. 89) found the western subspecies (*S. m. streckeri*) fairly common in thick mixed woods. Clark (1949, p. 260) caught seven in grass mounds in swamps; and four in gardens bordered by low ground.

*Mexican Pigmy Rattlesnake* (*Sistrurus ravus*).—This is a mountain rattlesnake, a resident of the tableland that surrounds Mexico City and extends east to the escarpment in Veracruz and southeast to Oaxaca. The association is largely the temperate pine-oak forest of Leopold (1950, p. 510). *S. ravus* has been collected at various altitudes between 6,000 and 10,000 feet. One specimen was caught at night in an open field (Davis and Smith, 1953, p. 142). In Puebla it was found in an area of porous soil with a growth of grass, agaves, cacti, small oaks, and thorny bushes; in Oaxaca in an area of mixed brush and forest, referred to by Goldman (1951, p. 229) as belonging to the Humid Upper Tropical Zone.

#### SUMMARY

As we review what has been said concerning the habitats to which the different kinds of rattlesnakes are addicted, we find that at least one kind occupies almost every type of habitat to be found in the United States and Mexico. Neglecting local limiting factors of food supply and the destructive activities of man, we can see that rattlers can and do survive everywhere, except where latitude or altitude, or both, have produced so short a season of adequate temperatures that the young cannot be brought to term, even in a two-year cycle. Rattlers can survive a very cold winter if it be not too prolonged; the only places in the United States where rattlers do not occur and where the winters are relatively mild are the coastal areas of northwestern California, Oregon, and Washington.

The greatest profusion of forms occurs in the central Mexican plateau area and its extension into Arizona. Some of these highland forms are restricted to the mountains, and, where the mountain ranges are not continuous, have become limited to montane islands. Other montane forms are able to extend their ranges to the plains, or possibly originated in the plains and gradually occupied higher elevations as well.

Aridity is less of a barrier than humidity; by and large more species and subspecies occupy dry than moist areas; and even in the mountains, arid zones are more likely to be tenanted than those of heavy rainfall and dense verdure, and by more different species. Species having the greatest ranges are those that prefer, in at least a part of their ranges, rocky hillsides or mountains with a scant brush cover.

That rattlesnakes may not thrive at altitudes to which they are unaccustomed is indicated by the following, from C. A. Knisly, Belgrade, Montana: "Carnival shows having snake dens, have trouble keeping their rattlers alive here, because of the high altitude. Most of them are western diamonds bought at Brownsville, Texas." Of course the fatalities may have been caused by other unfavorable conditions incident to captivity.

### ISLAND HABITATS

A considerable number of islands are inhabited by rattlesnakes. Although the insular populations are often similar to those of the nearby mainland, in other cases they have diverged to a noticeable extent, in a few instances to a sufficient degree to warrant recognition as distinct species. Some of the island populations, by their very differences, suggest that they have persisted there since the original separation of the islands from the adjacent mainland; others clearly represent more recent colonizations, having reached the islands by swimming, transportation on floating debris, by being carried by birds of prey, or by some similar means of dispersal. In some instances involving narrow straits, swimming produces a continual interchange of individuals between island and mainland. Occasionally islands have been found to be advantageous habitats, offering a better food supply or greater freedom from enemies. This, in some cases, has resulted in a heavier population on the island than on the adjacent mainland, or persistence after the mainland population has been exterminated. For example, in Michigan the most northerly specimens of the massasauga (*S. c. catenatus*) are found on Bois Blanc Island, in the Mackinac Straits; and the only timber rattlers (*C. h. horridus*) remaining in northern Ohio are on the tips of the Catawba and Marblehead peninsulas, and several of the adjacent islands in Lake Erie (Conant, 1938, p. 118; 1951, p. 118).

Islands inhabited by rattlesnakes represent various degrees of separation from the contiguous mainland. In some instances the separating water may be so narrow, so warm and well protected, as to offer virtually no barrier to creatures that swim as efficiently as do rattlesnakes. In these cases there will be a continual transference of individuals back and forth so that there is no true isolation, and thus no chance for insular differentiation.

Some of the inhabited islands are but little more than dry areas in swamps, or mounds in a general lowland. Such, for example, are Billy's, Bugaboo, and Minne Lake islands in the Okefinokee Swamp of southeastern Georgia, upon which Wright and Bishop (1915, p. 139) have reported. The canebrake rattler (*C. h. atricaudatus*) has been found on Billy's and Bugaboo, the eastern diamond-back (*C. adamanteus*) on Minne Lake, and the Carolina pigmy rattler (*S. m.*

*miliarius*) on Billy's. No doubt by swimming, or in the dry seasons, they all have ready access to any of these places. Similarly the western pigmy rattler (*S. m. streckeri*), the canebrake, and the eastern diamondback have been found at Avery Island, Louisiana, as I was informed by the late E. A. McIlhenny, although *adamanteus* may now be exterminated there.

The next degree of isolation is represented by the permanent water separations of rivers and lakes. Of the first I know of few examples, although there must be many. The South American rattler (*C. d. terrificus*) is found on the great Marajó Island in the delta of the Amazon—through the courtesy of D. Holdridge I have seen a photograph of a specimen taken there. At one time the massasauga occurred on Grosse Isle in the Detroit River (Baird and Girard, 1853, p. 15) but has now been exterminated there. Strecker (1908, p. 78; 1935, p. 27) has recorded both the western diamond (*C. atrox*) and western pigmy rattler (*S. m. streckeri*) on Mussel or Eichelberger's Island, North Bosque River, McLennan County, Texas. Several of my correspondents have mentioned finding rattlers on small unnamed islands in rivers, on which the snakes were resting while crossing the stream.

In lakes of small to moderate size, we have reports of the eastern massasauga (*S. c. catenatus*) on Pony Island, Indian Lake, Logan County, Ohio (Conant, 1938, p. 114); the Great Basin rattler (*C. v. lutosus*) on Anaho Island, Pyramid Lake, Washoe County, Nevada; the northern Pacific rattlesnake (*C. v. oreganus*) on Rattlesnake Island, Clear Lake, Lake County, California; and the sidewinder (*C. c. laterorepens*) on Echo Island, Salton Sea, Imperial County, California. I suspect that a good many rattlers (Mojaves, Panamints, or sidewinders) may still remain on some of the larger islands in Lake Mead (formed by Hoover Dam) although I found only one sidewinder when I hunted on a number of the smaller islands that were being pinched off by the rising waters of the reservoir in 1935.

No doubt many inshore islands of the Great Lakes are inhabited by rattlers. The timber rattler (*C. h. horridus*) occurs on South Bass Island (Ottawa County, Ohio) in Lake Erie (C. F. Walker, 1931, p. 11); and Morse (1904, p. 138) reported a small, declining colony on Mouse Island off Catawba Point in the same vicinity. The eastern massasauga (*S. c. catenatus*) inhabits a number of islands off the Michigan coast (Ruthven, Thompson, and Thompson, 1912, p. 128; Ruthven, Thompson, and Gaige, 1928, p. 133) including Charity, North, and Stony islands in Saginaw Bay, Lake Huron; and Bois Blanc Island in the Straits of Mackinac. G. C. Toner has written me that the same subspecies is found on several islands off the tip of Bruce Peninsula, between Lake Huron and Georgian Bay, Ontario, as well as on Fitzwilliam Island across the strait. J. R. Dymond has reported the massasauga on Payette Island, near Penetang, Simcoe County, Ontario; and Logier (1941, p. 103) mentions a specimen from Macdonalds (or Garrett) Island, Prince Edward County, but there is now some doubt as to the proper identification of this snake by the original observer. Mr. Logier later informed me of the presence of massasaugas on Arthur Island off the southeastern shore of Georgian Bay.

As might be expected, many of the low islands that fringe the coasts of Georgia and South Carolina are inhabited by rattlers. Thus the eastern diamondback has

been reported on Sapelo Island, McIntosh County, Georgia; and the canebrake on St. Simons Island, Glynn County, Georgia, and Johns Island, Charleston County, South Carolina. The Carolina pigmy rattler (*S. m. miliarius*) also occurs on the latter island. Without doubt many of the other islands that border the inland waterway are similarly tenanted by one or more of these three subspecies. The timber rattler (*C. h. horridus*) once inhabited Long Island but is now presumed to have been exterminated there (Englehardt *et al.*, 1915).

As might be expected of so excellent a swimmer as the eastern diamondback (*C. adamanteus*), aided by the favorable sea temperatures around Florida, this snake has colonized a number of the adjacent keys. I have a specimen from Key West. W. H. Fowler (1906, p. 110) has recorded it on Boca Chica, Big Pine, No Name, Summerland, and Sugar Loaf keys. Roger Conant writes that it is found on Rattlesnake Key off Terra Ceia; Clench (1925, p. 40) reports it on Sanibel Island; and Allen and Slatten (1945, p. 26) on Cudjoy (or Cudjoe) Key. Since the conditions of food and shelter are so favorable, no doubt these are but a few of the Florida islands that are occupied. The eastern diamondback has also been recorded on Cat Island, Harrison County, Mississippi. Even the little south-eastern pigmy rattlesnake (*S. m. barbouri*) has been observed on one island—Paradise Key, Dade County, Florida—although Allen and Neill (1950, p. 10) consider it rare in the keys. The western pigmy rattler (*S. m. streckeri*) has been found on Cat Island in Mississippi Sound, Mississippi (Smith and List, 1955, p. 124). Off the coast of Texas, across Aransas Bay from the mainland, both the western diamond (*C. atrox*) and the western massasauga (*S. c. tergeminus*) have been found on St. Joseph Island.

On the Pacific Coast, the offshore waters are both deeper and colder than on the Atlantic or Gulf of Mexico coasts. Rattlers are found swimming at sea much less frequently and it is extremely doubtful that there is any interchange—or has been for a long time—between the insular or mainland populations. This statement is probably true of all the islands known to be inhabited by rattlers in this region except Morro Rock, Magdalena, Santa Margarita, and Tiburón. Not only are the Pacific and Gulf of California islands separated from the mainland by greater water barriers, but they are ecologically more differentiated from the mainland than are the Atlantic and Gulf islands.

On the Pacific Coast of California, two islands are tenanted by rattlesnakes—Morro Rock by the northern Pacific (*C. v. oreganus*) and Santa Catalina by the southern Pacific (*C. v. helleri*). Although more fog-shrouded than the mainland, these islands have a good brush cover and considerable rock, so that the surroundings are not greatly different from some niches on the mainland.

Proceeding down the coast of Baja California we have, on South Coronado, the indigenous subspecies *C. v. caliginis*; on Cedros, the indigenous species *C. exsul*, which will be mentioned further; on Magdalena, *C. e. enyo*; and, on Santa Margarita, three species, the San Lucan diamond rattler (*C. r. lucasensis*), the Lower California rattler (*C. e. enyo*), and the speckled rattlesnake, probably the San Lucan subspecies (*C. m. mitchelli*). The classification of the latter cannot be verified since only one specimen has been collected there and this was lost in the San Francisco fire of fifty years ago. However, there is no reason to doubt the presence of this rattler on the island, as its barren, rocky nature is ideal for

*mitchelli*. The adjacent Magdalena Island is lower and flatter, with fewer rocky hills; only *C. e. enyo* is known to occur there.

The islands of the Gulf of California are more plentifully and more generally populated by rattlers than those of the Pacific Coast. Table 2:5 shows the distribution of the snakes among these islands. There are, altogether, 13 subspecies of rattlesnakes scattered among 19 islands. Most of these Gulf of California islands answer to a common description—they are rocky (volcanic), barren, with peaks of considerable altitude. Sparse brush and cacti are present; water is available on a few. San José and Tiburón probably have greater areas with a heavy cover of vegetation than the others. It may be expected that future explorations of these desolate islands will disclose additional species on those now known to have at least one rattler; and that several of the other islands, from which no rattler records are yet available, will be found to harbor them. There are rumors of rattlers on several others.

All of the islands contain the species that would be expected on geographical grounds. The islands nearest to the Baja California peninsula have Baja Californian forms; the two nearest Sonora (Tiburón and San Esteban—the latter via Tiburón) have Sonoran forms. The rattler on the only island that is equidistant from both shores has differentiated sufficiently from its nearest relatives to be accorded specific distinction; this is the Tortuga Island diamond rattler (*C. tortugensis*). However, it more nearly resembles the western diamond (*C. atrox*) of Sonora than the red diamond (*C. r. ruber*) across the Gulf in Baja California.

Island forms are often stunted compared with their mainland congeners. This is clearly true of the rattlesnakes (*C. v. caliginis*) of South Coronado, the Cedros Island diamond (*C. exsul*), the Santa Catalina Island diamond (*C. catalinensis*), the Tortuga Island diamond (*C. tortugensis*), the El Muerto Island speckled rattler (*C. m. muertensis*), and the red diamonds of Ángel de la Guarda. But, strangely enough, the largest speckled rattler available from any source is from Ángel de la Guarda, and this is particularly notable in view of the few island specimens that have been collected, compared with the large number from the mainland.

To date, four island rattlesnakes have been accorded recognition as full species, owing to their considerable differentiation from their mainland prototypes. These are:

The Cedros Island diamond rattler (*C. exsul*) from Cedros Island, Pacific Coast of Baja California; nearest mainland relative, the red diamond (*C. r. ruber*)

The Santa Catalina Island diamond rattler (*C. catalinensis*) from Santa Catalina Island, Gulf of California; nearest mainland relative, the San Lucan diamond (*C. r. lucasensis*)

The Tortuga Island diamond rattler (*C. tortugensis*) from Tortuga Island, Gulf of California; nearest mainland relative, the western diamond (*C. atrox*)

The Aruba Island rattlesnake (*C. unicolor*) from Aruba Island, off the coast of Venezuela; nearest mainland relative, the South American rattler (*C. d. terrificus*)

All four are stunted compared with their mainland relatives. The last three live under conditions more arid than those characteristic of the centers of the mainland populations. However, this is not true of Cedros Island, which does not differ greatly from some of the mainland areas inhabited by the red diamond. As a matter of fact, there is a considerable ecological range on Cedros, for part is barren, and part fertile and quite humid. There are rocks, heavy brush, and

even trees in the canyons and at the higher elevations. But notwithstanding this ecological similarity, the separation from the mainland has been so long that a notable differentiation has occurred. Aruba was forested in pre-Columbian times, but is now relatively barren. All four of the islands that harbor distinct species are so situated that any exchange of individuals with the mainland has been virtually impossible for a long time.

Four island populations have differentiated enough from their mainland prototypes to warrant nomenclatorial recognition as subspecies. These are:

The Coronado Island rattlesnake (*Crotalus viridis caliginis*) from South Coronado Island off the northwestern coast of Baja California; nearest mainland relative, the southern Pacific rattlesnake (*C. v. helleri*)

The Cerralvo Island rattlesnake (*C. enyo cerralvensis*) of Cerralvo Island, Gulf of California, Mexico; nearest relative, the Lower California rattlesnake (*C. enyo enyo*) of the central and southern sections of the peninsula of Baja California

The San Esteban Island rattlesnake (*Crotalus molossus estebanensis*) of San Esteban Island off Tiburón Island near Lat. 29° N., in the Gulf of California; nearest relative, the northern black-tailed rattler of Tiburón Island and the adjacent mainland of Sonora

The El Muerto Island speckled rattlesnake (*Crotalus mitchelli muertensis*) of El Muerto Island in the San Luis group, off the Baja California coast at Lat. 30° N., in the Gulf of California; nearest mainland relative, the southwestern speckled rattlesnake (*C. m. pyrrhus*)

The propriety of awarding subspecific recognition to island populations is doubtful, when territorial intergradation with other subspecies is obviously impossible. For technical reasons, some taxonomists feel that an island population should be given either a full specific status or no recognition. However, I favor a subspecific status, where warranted by the degree of differentiation, because the resulting name serves to indicate relationships. Almost all the island snakes of the Californias have differentiated in some degree from their mainland prototypes, and additional subspecies may be described as more specimens become available. Among those most closely approaching this distinction are the red diamonds of Ángel de la Guarda, the red diamonds of Monserrate, and the speckled rattlers of Espíritu Santo, in the Gulf of California.

## POPULATION FACTORS

### POPULATION DENSITIES

Trustworthy figures on actual population densities of rattlers are scarce indeed, owing to the obvious difficulty of making accurate censuses. The most complete studies thus far have been those on the northern Pacific rattlesnake made by Fitch and his associates on the San Joaquin Experimental Range in Madera County, California. Horn and Fitch (1942, p. 120; see also Wagnon *et al.*, 1942, p. 73) reached the conclusion that there was somewhat in excess of one rattlesnake per acre on this rolling cattle ranch. Fitch (1949a, p. 546), after a resurvey of this and some additional data, attained a figure of 1.19 rattlesnakes per acre. The studies were made by capturing, marking, and releasing rattlers and subsequently recapturing them. It was then possible, by calculations involving the ratio of the recaptured snakes to those newly taken for the first time, together

with data on the distances traveled by the recaptures in the interim, to estimate the total population with some accuracy. Probably this release and recapture method, as discussed by Dice (1938, p. 119),<sup>4</sup> is the only satisfactory one for secretive creatures such as rattlesnakes, which lie hidden down holes or in rock crevices much of the time. Such a program, to yield dependable results, requires several years for its completion.

Fitch points out that, even in a territory as small as the Experimental Range (4,600 acres), there is a considerable variation in the population density in different parts of the area investigated. A. M. Jackley reported a similar nonuniform distribution of prairie rattlesnakes in South Dakota:

I made an effort for a number of years to check on the summer distribution. What I had in mind was to get some basis upon which I might venture an estimate of our rattlesnake population. I finally gave it up as useless for the following reasons: I could choose an area of, say, 1,200 acres and prove the population to be as high as 1,200, or one to the acre, but even within such an area in all probability 75 per cent of this number would be confined to one section, or 640 acres. Or, I could choose an equal area adjoining this wherein there probably would not be more than 200. Again, I could find restricted areas where the population would be heavy and adjoining it would be equal areas with no rattlers at all. There is much local variability, even in prairie country.

Interesting, although less conclusive, figures may be secured by a thorough survey of a limited plot. For example, Floyd C. Morris of the U. S. Soil Conservation service at St. Joseph, Louisiana, reported that, when a 30-acre field was cleared of second-growth gum, oak, pecan, and hackberry in August, 28 canebrake rattlers (*C. h. atricaudatus*) were discovered in the course of the work.

Unfortunately, when rattlesnake control measures are undertaken, there is usually no record kept, either of the area covered or the thoroughness with which it has been searched. And, regardless of the care exercised in hunting, the snakes in mammal holes or other hiding places will not be discovered. But, although they will not have the usefulness of population-density statistics, it will be worth while to cite some figures indicating the extent of populations, avoiding data involving den concentrations, the misleading nature of which is pointed out elsewhere.

A rancher in Texas in clearing brush killed 60 rattlers per square mile; another killed 77. Gowanloch (1934, p. 10) mentions the killing of 4,389 rattlesnakes on one tract in connection with the Mediterranean fruit fly eradication campaign in Florida. Stoddard (1942, p. 436) stated that 1,000 eastern diamondbacks (*C. adamanteus*) were killed per annum on seven hunting preserves in the Thomasville-Tallahassee region, where a bounty of one dollar had been offered for each snake. Ross Allen advised me that over a period of 28 years he had received from 1,000 to 5,000 eastern diamondbacks per annum at his snake exhibit at Silver Springs, Florida, with a grand total of about 50,000. These figures give some idea of the commonness of this large rattlesnake in parts of Florida. According to Fonseca (1949, p. 325) the South American rattlesnake (*C. d. terrificus*) is, with the single exception of the pit viper known as the jararaca (*Bothrops jararaca*), the most plentiful venomous snake in Brazil. In the course of 45 years, 115,114 specimens of *terrificus* were received by the Butantan Institute, at São Paulo, Brazil.

<sup>4</sup> Some herpetological references to investigations of this character, a few of which included rattlesnakes are given on p. 571.

Some of my correspondents, on the other hand, have commented on how few rattlesnakes they have seen, although their work frequently took them into rattlesnake-infested country. The experienced naturalist Vernon Bailey (1905, p. 50) stated that although the western diamond rattler was often reported as excessively common in Texas, in the course of his field work he never found more than a dozen individuals in their favorite haunts, during a season's work of four or five months.

The late Joseph S. Dixon, field naturalist of the U. S. Fish and Wildlife Service, had kindly given me the following information about his experience:

On July 11, 1940, three northern Pacific rattlesnakes were found on a warm rocky slope between Poison Lake and Swamp Lake in an area 50 feet wide and less than half a mile long. This makes the second day that we have found three rattlesnakes in half a day's hike in this region, with a total of eight rattlesnakes found in six days on less than three square miles. This represents about the maximum rattlesnake population that I have encountered in the Sierra Nevada in 30 years of field work and is much higher than any rattlesnake population that I have ever found in Death Valley, or in the Colorado or Mojave deserts.

It should be stated, with regard to Dixon's catch, that it represented the results of an intensive hunt by 25 trained naturalists.

I have already discussed island populations of rattlesnakes. Although many islands are reputed to be "alive with rattlesnakes" such reports are generally exaggerated, and it is usually found that the population density is not conspicuously different from that of similar areas of the mainland. However, there are three islands, El Muerto, Tortuga, and Monserrate, all in the Gulf of California, that have really heavy concentrations, as has been demonstrated by several collectors, for considerable numbers have been taken on each island on relatively short visits. These are, in fact, the only islands off Baja California—although many others harbor rattlers—where a collector of experience would be sure to obtain a number of snakes in a single day's hunt. Steve Glassel told me, just after a visit to Tortuga in December, 1934, that the indigenous diamondbacks (*C. tortugensis*) were seen every 100 to 150 feet. One collecting party secured 20 specimens in two hours of collecting. The snakes disclosed their presence by rattling if a rock under which they were hiding was rapped. Nelson K. Carpenter stated that the concentration on that island was greater than he had ever seen elsewhere, and that he and his associates on a bird-nesting expedition actually left the island for fear someone might be bitten. He also remarked on how plentiful *C. m. muertensis* was on El Muerto Island, a situation verified by subsequent collectors. F. S. Cliff reported the tracks of *C. r. ruber* very common on Monserrate, and many of these rattlers have been collected on that island.

#### EFFECT OF DENS ON POPULATION ESTIMATES

In those areas where rattlesnakes congregate from considerable distances for purposes of hibernation, particularly if the den locations are accessible to people, it is very difficult to get truly objective estimates of population densities on the summer range. It is rarely understood that the conspicuous concentrations observed at the dens are drawn from wide areas, aggregations to be noted only for a few days in the fall or spring, and that these are by no means representative of the population density anywhere during the seasons of normal activity. It is but

natural that a person happening upon a den at the appropriate time would conclude that the entire country must literally swarm with rattlers, whereas he might travel for days, after they had scattered for the summer, and rarely see a single one. There is little doubt that the published reports of the great numbers of rattlers in some parts of the West in the early days were based on such observations at dens. Even today the stories of increasing populations of rattlers seem usually to be premised on the greater publicity now being given to the discovery of dens.

Some of the published reports, probably having den concentrations as their bases, were the following: Sullivan (1852, p. 174) said the rattlers along the banks of the Mississippi were fabulous in number. Allen (1874, p. 69) stated that in the North Pacific Railroad Expedition of 1872 about 2,000 prairie rattlers were killed in the Bad Lands of the Little Missouri and along the Yellowstone, but fewer were found on a subsequent expedition one or two years later. One may hazard the guess that the first expedition came upon the dens at the most propitious time. Yarrow and Henshaw (1878, p. 1633), on Rattlesnake Hill in southern New Mexico, saw between 300 and 500 rattlers on October 5, and killed 79. Chittenden (1903, p. 47) reports having killed 130 rattlers in the course of a few minutes near Bijou Hills, Brule County, South Dakota. He repeats (1935, p. 826) that in some areas they were present in prodigious numbers. Mrs. Simcoe (1911, p. 200), in a diary written in 1793, mentions 700 rattlers that were killed by surveyors, near Burlington, Ontario. Morse (1927, p. 217) saw about 100 northern Pacific rattlers (*oreganus*) on a single flat rock on the banks of the Yuba River in California, in the early gold-mining days. Anon. (1937, p. 207) quotes, from the *Concordia* (Kansas) *Empire* of October 20 and 27, 1876, descriptions of a large den said to be situated on a hill 8½ miles southwest of the town. Up to 3,600 snakes had been killed there, of which 1,776 were blue racers; rattlers were not mentioned. Dodge (1938, p. 50) remarks that considerable concentrations of rattlers may be encountered in the autumn while they are en route from their summer ranges to the dens.

My own correspondents have commented on the different impressions one may gain of rattlesnake populations when comparing den concentrations with the frequency with which the snakes are to be seen at other times. C. B. Perkins, visiting the Platteville, Colorado, dens at weekly intervals during the summer, collected only two rattlers at these prairie-dog towns, where hundreds were later in evidence while entering or leaving hibernation. Sweet (1954, p. 54) said he secured more rattlers in a single day at one of the dens in Montana than in an entire season on the summer ranges of the snakes.

Rev. A. C. Mackie, of Vernon, British Columbia, expresses somewhat the same thought:

A description of my fruitful experience at dens might lead to the idea that this locality is infested with rattlesnakes and is undesirable as a residential centre. Such is not the case. They are very localized and their pursuit entails a good deal of physical effort and energy. Many people who have lived here for thirty years have yet to see their first one.

I have mentioned elsewhere (p. 581) some statistics on den populations as indicated by actual catches at dens.

The effect of dens on estimates of snake populations, as reported by early explorers and trappers, may be misunderstood even today. Thus Buley (1950, vol. 1, p. 256) remarks that the early statistics of snake hunts are astonishing to people a century later. It is, of course, true that rattlers have been practically exterminated in many agricultural areas, but in the wilder districts they are about as numerous as ever. But the diaries of the forty-niners and the other westward migrants naturally dwelt upon swarming den concentrations when they came upon them, and thus one gains the impression of large populations. Diaries of days other than during the snakes' lying-out periods of fall and spring seldom mention encountering more than five or six rattlers in a day. But there were exaggerations in the other direction, as, for example, when Edwards (1836, p. 76), in a guide to Texas prepared for emigrants, farmers, and politicians, remarks: "Such is the rattlesnake, fortunately not often to be met with in Texas."

#### RARITY OF PARTICULAR SPECIES

It goes without saying that some rattlesnakes are less common than others, less common even in their areas of greatest abundance. But it is doubtful that any is rare in the sense of being really few in numbers throughout its range. For, any species, to survive occasional but temporary adverse conditions of disease or a reduced food supply, must have a certain reservoir of numbers, such that fluctuations in population will never reach a minimum beyond which recovery is impossible, for once such a minimum is reached, extinction is inevitable.

There are subspecies of rattlesnakes—*miquihuanus*, *vegrandis*, and *oaxacus*, for example—of which but two or three specimens have ever been secured for study by scientific institutions. But, so far as we know, these subspecies are rare only because the places where they live are difficult of access; there is no reason to believe that specimens could not be collected in considerable numbers if one could readily reach the localities where they occur.

In some cases it may be necessary to discover new techniques of collecting, for the history of herpetology is replete with instances of species thought to be rare until someone discovered a new method of hunting that showed them to be common and resulted in generous catches. One type of rarity that is real exists along the fringe of an animal's range. Most creatures, as they approach whatever ecological barriers limit their further migration, tend to thin out, unless the change in conditions at the barrier be an exceedingly steep or sudden one.

As the scarcity of specimens of certain kinds of rattlers may be of popular interest, I give herewith a list of those forms of which fewer than ten specimens have been available to me in this study: *C. basiliscus* *oaxacus* (2), *C. catalinensis* (1), *C. durissus* *vegrandis* (2), *C. enyo* *cerralvensis* (2), *C. enyo* *furvus* (4), *C. molossus* *estebanensis* (3), *C. pricei* *miquihuanus* (3), *C. scutulatus* *salvini* (8), *C. stejnegeri* (5), *C. transversus* (3), and *C. willardi* *meridionalis* (7).

#### CYCLES OF ABUNDANCE

It is well known that there are cyclic fluctuations in the populations of many animals, including birds and mammals—cycles of longer periods or swings than mere seasonal effects. These cycles are usually caused by fluctuations in food supply, or by the incidence and virulence of disease. There are obvious relationships

between the cyclic variations in the populations of predators and prey. But sometimes the causes of population fluctuations are neither simple nor clear.

Although the abundance of rattlesnakes, like that of other predators, must fluctuate with the abundance of prey, it is probable that they are less quickly or sharply responsive to changes in the food supply than is the case with mammals and birds; for they feed with greater irregularity and are able to withstand, if they must, fasts measured in terms of months, not only during hibernation, but in seasons of normal activity. Many of my correspondents believe cyclic variations to be evident—variations of a type not to be confused with long-term trends caused by changes in vegetation and refuges resulting from human activities. However, actual quantitative proofs are not available, for years of study would be necessary to supply accurate information for a single area. It is probable that many of the opinions on cyclic fluctuations are more subjective than objective and may result from chance encounters or from seeing the snakes lying about their dens at hibernating time.

Rattlesnakes are plentiful here, my trail crews having disposed of 30 in 1935, but found very few in 1936. *Report from Soda Springs, Calif.*



The hordes of Mormon crickets infesting this area since 1934 have caused rattlesnakes to change their ranges [presumably because of the effect on the food supply]. *Report from Lamoille, Nev.*



In certain years rattlesnakes seem to be more numerous, and then they disappear for awhile. *Report from Teamah, Nebr.*



Some years rattlers are plentiful, other years they disappear, or do not come out. *Report from Cimarron, Kans.*



The question often asked is: "Does the increase or decrease in our rattlesnake population occur in cycles?" Such is the case with many creatures, particularly insects and small rodents such as mice. This subject has been carefully studied over a period of 16 years, and no evidence has been obtained that suggests sudden and large increases at regular intervals. There is one thing that deserves mention, which is that the snakes are more in evidence when weather and temperature are most agreeable to them. Under all conditions that are uncomfortable to them, they remain concealed. This explains why more are encountered one year than another, even though the population remains the same. *A. M. Jackley, Pierre, S. Dak.*

It is my conclusion that there are probably rattlesnake cycles of abundance, following similar cycles affecting their prey, but that the peaks and valleys are less accentuated than in the prey cycles. However, a definite proof of such cycles is not yet at hand. Rattlesnakes do not seem to be subject to devastating epidemics of disease, at least none has been brought to my attention. However, it is true that an occasional rattler is found, showing, by its wasted condition, that it is suffering from some disease, and, since other snakes in the same area are not in the same condition, the trouble cannot be attributed to a regional food shortage.

#### POPULATION TRENDS

As has been discussed under control (p. 1024), the persistent enmity of man and his domestic animals usually results in a sharp decrease in rattlesnake populations about human habitations. This has been a common observation since colo-

nial times. It is only where there is some inaccessible refuge that can serve as a reservoir—some rocky cliff, impenetrable marsh, or dense expanse of chaparral—that rattlers are able to maintain themselves near populous places. When they fail, a decline is to be expected, even though the agricultural activities of man may serve to sustain an increased food supply in the form of a larger rodent population.

This is not true of all snakes; for example, the Sonoran gopher snakes (*Pituophis catenifer affinis*) and the red racers (*Masticophis flagellum piceus*) have increased many fold in the Imperial Valley of California since the advent of irrigation, as can be easily proved by comparison of their numbers within and beyond the cultivated area (Klauber, 1939a, p. 51). But the indigenous rattlesnakes, the western diamond (*C. atrox*) and the Colorado Desert sidewinder (*C. c. laterorepens*), have been unable to accommodate themselves to the new conditions—the grapefruit groves, and lettuce and alfalfa fields that seem to us so much more attractive than the barren desert—and are almost never found within the cultivated area. Nor is this due to lack of food, for various rodents fatten and multiply on the farmer's crops.

Many of my correspondents have commented upon the gradual disappearance of rattlesnakes because of the encroachments of agriculture, cattle and sheep grazing, the clearing of forests, and other human activities. These statements come from all sections of the country, and relate to all species that live in habitats serving man's purposes:

Observations over 25 years lead me to believe that the snake population is gradually diminishing. This is only to be expected as a result of the increasing human use of this area. *Frank McCaslin, U. S. Forest Service, North Bloomfield, Calif.*



Twenty years ago there were hundreds, even thousands, of rattlers on the south slope of Red Mountain (across the river from Rich Bar, Plumas County) where now they are very scarce. *J. L. Stinnett, Feather River Fish Hatchery, Clito, Calif.*



The continuous killing of the snakes and the cultivation of large areas for wheat have driven the rattlesnakes out of extensive areas. As you probably know, in every country inhabited by rattlers there were sections where none apparently existed. Whether this was due to some natural enemy, or some other condition generally distasteful to the snakes, is not known. *F. F. Wehmeyer, U. S. Forest Service, Heppner, Oreg.*



In the foothills southeast of McMinnville rattlers were once common, but they have now become very scarce. *James A. Imlah, McMinnville, Oreg.*



Old-timers claim that there has been a marked decrease in the number of rattlers in the past 25 years due to eradication by man. *W. E. Wheeler, Cle Elum, Wash.*



In places along the Okanagan that are thickly settled, the rattlesnake population is being exterminated and around many of the towns a rattlesnake is something of a rarity. *C. F. Kearns, British Columbia Game Department, Nelson, B. C.*



Rattlesnakes are quite scarce now due to the prairie being plowed. I personally killed 32 rattlers in 1921, but have not seen one for two years. *Fred W. Fowler, Ulysses, Kans.*



Rattlers are not so numerous as in previous years before the sod was broken. *Lee A. Hunter, Sublette, Kans.*

Rattlesnakes formerly were very numerous, but disc tillage tools have greatly reduced their numbers. *Claude F. Wright, Hugoton, Kans.*



Rattlesnakes are not to be found around here now. Only once in a great while do you find one, although 30 years ago they were quite numerous. *Theodore R. Jones, Wayne, Nebr.*



The major portion of the county is tillable. Snakes of all types have been driven into the territory along South Blue River, 15 miles north of here. *Glen F. Felix, Geneva, Nebr.*



One rattlesnake was found on a porch two miles from Tyndall. However, rattlers in this county are indeed very rare. They have become practically extinct in the entire eastern part of South Dakota. *Carl A. Lehman, Tyndall, S. Dak.*



Rattlesnakes disappeared after the cultivation of the soil. There were many here 50 years ago. *O. A. Nelson, Ruby, N. Dak.*

Some correspondents merely call attention to the fact that their observations are confined to agricultural land, taking it for granted the reader will understand that rattlers are not prevalent in such situations:

This station is located in a heavily populated agricultural district and I have not observed rattlers within several miles of the fish hatchery. *Merrill Brown, Central Valleys Fish Hatchery, Elk Grove, Calif.*



Most of my patrol district is delta land [intensively cultivated], so I do not see many rattlers. *H. S. Vary, Game Warden, Sacramento, Calif.*



I have seen only one rattlesnake in this county—most of which is cultivated—in a year and a half. *H. C. Jackson, Game Warden, Santa Ana, Calif.*



Rattlesnakes have been rather scarce during the 30 years I have lived here. The natives claim that hogs have killed them out. I rather think that timber workers have killed them off as the country has been worked over within the last 50 years. *James S. Connelly, U. S. Forest Service, Bardley, Mo.*



We have the timber rattlesnake in the mountains of Virginia. It is my impression that its population has lessened during the past ten years that I have been here. Some people are inclined to think it increasing, but such reports come from summer campers whose locale is the immediate vicinity of the small mountain rivers. There have been two dry summers in a row and I attribute the sight of snakes to their seeking water. *Meredith Leitch, Staunton, Va.*



The wholesale destruction of timber in this section of the country is probably responsible for the scarcity of rattlesnakes. My work carries me throughout the state and there are very few places outside the mountainous sections of the state where anyone has seen a rattler in a long time. *Glenn Gentry, State Division of Game and Fish, Paris, Tenn.*

Some published statements, emphasizing the same downward trend in population that my correspondents have mentioned, have been the following: Beverly (1705, p. 63), Bartram (1744, p. 358), Kalm (1752–53, p. 312; 1758, p. 286), Pen-  
nant (1787, p. 88), Merrill (1817, p. 17), Hurter (1893, p. 258), Beyer (1900, p. 29), Wiffen (1913, p. 950), Brimley (1917, p. 182), Babcock (1925, p. 8), Ingles (1929, p. 71), Cook (1943, p. 52), and Loomis (1948, p. 122). Bullock (1827, p. xxviii)

went so far as to state that rattlesnakes were becoming as great a curiosity about the towns of America as in England; and Hartwig (1873, p. 298) thought that rattlesnakes would probably be extinct within a century or two.

There have been a few dissents from the general opinion that rattlesnake populations are decreased by human activities. Behr (1888, p. 95) thought Pacific rattlers were on the increase in some sections of California because of the destruction of their natural enemies. Githens (1935b, p. 163) expressed the opinion that the rattlesnake population was expanded by the effects of agriculture and this may be true of the western diamonds (*C. atrox*) in some parts of Texas.

One correspondent calls attention to an increase in rattlesnakes following a reduction in control measures:

Rattlesnakes are much on the increase in this area, Lycoming and Sullivan counties being the section I patrol. I believe the reason for the increase is the absence of the CCC boys who killed a great many while working in the woods; also, the absence of forest fires during the past five years. For the last 10 years I averaged about 8 killed per year. I base my statement that they are on the increase on the fact that I killed 29 so far this year. If anything, my activities have been more limited this year than before. *C. A. Bidelspacher, State Fish Warden, Williamsport, Pa.*

We may summarize the more important population-reducing agencies that are incidental to agriculture and other human activities as follows: Elimination of refuges and cover, such as rock piles, fallen trees, brush, marshes, and rodent holes; increase in domestic animal enemies, particularly dogs and hogs; reduction in food supply by rodent control; direct destruction by agricultural machinery, especially the disc plow and mowing machine; and the installation of smooth-surfaced, high-speed roads, fatal traps for almost every snake crossing when the traffic is heavy.

#### PROPORTION OF RATTLESNAKES IN SNAKE POPULATIONS

In many areas, rattlesnakes are the commonest of snakes; indeed in some they may exceed all other kinds combined. Unfortunately, accurate population statistics covering snakes of all kinds are lacking except from a few areas, and even from these, the results can only be approximations, so different are species of snakes with respect to size and conspicuousness. Necessarily, the smaller types and the fossorial forms are seldom fairly represented in a census.

Uhler, Cottam, and Clarke (1939, p. 607) collected snakes in the George Washington National Forest of Virginia for the purpose of studying their food habits. Timber rattlesnakes (*C. h. horridus*) were the most numerous of all snakes, numbering 253 out of 885, or 28.6 per cent. Horn and Fitch (1942, p. 100) judged the northern Pacific rattlesnake to be the commonest snake on the San Joaquin Experimental Range; in fact, Fitch (1949a, p. 513) believed it to exceed all other snakes combined. Fautin (1946, p. 293), in the northern desert-shrub association of western Utah, found rattlesnakes (*C. v. lutosus*) to comprise 40.4 per cent of all snakes encountered; in the shad-scale and tetradymia communities they made up 78.9 per cent.

A. M. Jackley, from his observations in South Dakota, believed the prairie rattlesnakes (*C. v. viridis*) to be the commonest snake in that state. In fact, the great concentrations of prairie rattlers at the beginning and end of the denning season has led to a general belief upon the part of observers, no doubt justified, that

they are more numerous in most of the territory they inhabit than any other snake. Allen (1874, p. 69), speaking of the Little Missouri and Yellowstone rivers, and Root and Connelley (1901, p. 251), describing conditions along the South Platte, expressed the opinion that the rattlers outnumbered all other species of snakes combined.

In our San Diego County snake census, involving 12,917 snakes collected or observed during the years 1923-38, inclusive, the zonal proportions of rattlesnakes, expressed as percentages of all the snakes from each zone, were found to be as set forth in table 8:1.

TABLE 8:1  
SAN DIEGO COUNTY RATTLESNAKES: PERCENTAGES OF TOTAL SNAKE POPULATION IN EACH ZONE

Species	Zone							Total as a percentage of all snakes
	Coast	Inland valleys	Foothills	Moun-tains	Desert foothills	Desert	Zone undeter-mined	
Colorado Desert side-winder ( <i>C. c. latero-repens</i> ).....	.....		.....		3.0	20.9		1.2
Red diamond ( <i>C. r. ruber</i> ).....	6.6	10.6	8.3	1.1	9.1	1.5	4.1	7.8
Southwestern speckled ( <i>C. m. pyrrhus</i> ).....	*	1.5	5.8	4.6	5.7	0.5	1.4	2.5
Southern Pacific ( <i>C. v. helleri</i> ).....	10.9	11.1	8.0	17.1	6.3	....	30.0	9.7
Total rattlesnakes....	17.5	23.2	22.1	22.8	24.1	22.9	35.5	21.2

\* Less than 0.1 per cent.

It will be observed that, although the relative proportion of the several species varies from zone to zone, the total proportion of rattlers remains about 20 per cent of the entire snake population.

One of the most fruitful methods—and probably the most accurate one—of checking composite snake populations in the desert is to drive on paved roads and count the snakes found thereon, whether alive or dead. Even small, nocturnal forms like the desert leaf-nosed snake (*Phyllorhynchus decurtatus perkinsi*) or the fossorial desert worm snake (*Leptotyphlops humilis cahuilae*) will be found in appropriate numbers. However, the trips must be repeated at all seasons, and both day and night, if representative data are to be obtained. With several associates and collaborators, I have made such investigations in two areas. The first was on the edge of the Colorado Desert in the Borrego section of western San Diego County. Out of 827 snakes of all kinds, the Colorado Desert sidewinder (*C. c. laterorepens*) constituted 5.9 per cent, the red diamond (*C. r. ruber*) 1.9 per cent, and the southwestern speckled rattler (*C. m. pyrrhus*) 0.2 per cent, or a total for all three rattlers of 8.0 per cent of the entire snake population.

In the second investigation, in the western Mojave Desert (the Mojave-Palmdale-Adelanto-Kramer area), out of 605 specimens, the Mojave Desert sidewinder (*C. c. cerastes*) proved to be the most plentiful snake, comprising 21.7 per cent of

the total; the Mojave rattler (*C. s. scutulatus*) made up 12.9 per cent, bringing the total for both rattlers to 34.6 per cent. This proportion is probably representative of those sections of our western deserts where the small genera such as the leaf-nosed snakes (*Phyllorhynchus*) or the shovel-noses (*Chionactis*) are not so prevalent as they are in the warmer and lower-altitude areas farther south.

#### COMPOSITE POPULATIONS

There are extensive areas of the United States and Mexico in which two or more species of rattlesnakes occur together. Sometimes they occupy the same ecological niche; in other cases a careful survey will reveal slight separations. It is particularly profitable to study the conditions along the edges of the ranges of two overlapping species, for here the slight territorial differences that permit one species to extend its range beyond that of another may be clearly manifest.

In some cases, two species may be competitors for food; in others, differences in size or food preferences may make them virtually independent of each other. For example, the largest and one of the smallest of rattlesnakes—the eastern diamondback (*C. adamanteus*) and the southeastern pigmy rattler (*S. m. barbouri*)—are found together in many parts of Florida, but their competition for food cannot be serious, for only with respect to mouse-sized creatures do the food requirements of the smallest *adamanteus* and largest *barbouri* overlap. On the other hand, in western San Diego County, California, three species of quite similar size and food habits—the red diamond (*C. r. ruber*), southern Pacific (*C. v. helleri*), and southwestern speckled rattlers (*C. m. pyrrhus*)—are found together, and are certainly food competitors.

In some instances, composite populations are more apparent than real. Range maps indicate that in extreme southeastern Arizona—eastern Pima, Santa Cruz, and Cochise counties—no less than 11 species and subspecies of rattlers are to be found: the Mojave (*C. s. scutulatus*), western diamond (*C. atrox*), prairie (*C. v. viridis*), Arizona black (*C. v. cerberus*), tiger (*C. tigris*), banded rock (*C. l. klauberi*), northern blacktail (*C. m. molossus*), Sonoran Desert sidewinder (*C. c. cercobombus*), Arizona twin-spotted (*C. p. pricei*), Arizona ridge-nosed (*C. w. willardi*), and western massasauga (*S. c. tergeminus*). But it is doubtful whether more than 5 or 6 of these actually occur in any one place. There are mountain areas where *molossus*, *klauberi*, *pricei*, and *willardi* are to be found together; prairies inhabited by *scutulatus*, *atrox*, *viridis*, *molossus*, and *tergeminus*; and deserts inhabited by *scutulatus*, *atrox*, *tigris*, *molossus*, and *cercobombus*. But even where the snakes live so near each other that their trails must often cross in their wanderings, it is probable that their ecological preferences insure a considerable degree of separation. For example, of the 5 desert forms last mentioned, *tigris* and *molossus* prefer rocks, whereas the others favor sand. Similarly, in western San Diego County, *pyrrhus* prefers rocks, *ruber* rocks and cacti, while *helleri* is more catholic, being equally at home in these, as well as in chaparral or grass. From these remarks no one should presume that these snakes avoid, as if contaminated, the kinds of surroundings I have stated they do not prefer; on the contrary, they are found in such places with moderate frequency. But when the kinds of cover they prefer are completely absent, then one is likely to discover that the snake favoring that niche has also disappeared or has become quite rare. Thus, in western San Diego

County, in the coastal and inland valley belts, granite outcrops are scarce or absent, and so also are the speckled rattlers (*pyrrhus*). Similarly, in the desert, although sidewinders are not infrequently found in rocky situations, they tend to disappear where the sandy washes threading through the tumbled boulders have narrowed to mere streaks.

Of course, problems of occupancy and population density are often not to be settled entirely as indicated by ecological preferences. For example, the Chiricahua and Huachuca mountains of southeastern Arizona are quite similar in character and cover. Both are inhabited by the little mountain species, the Arizona twin-spotted rattler (*pricei*) and the banded rock rattler (*klauberi*). But the former is much the more numerous in the Chiricahuas, whereas this condition is reversed

TABLE 8:2  
DISTRIBUTION OF A COLLECTION OF RATTLESNAKES IN CENTRAL ARIZONA

Subspecies	Station						Total
	Ramsgate	Skull Valley	Kirkland	Hillside	Date Creek	Congress Junction	
Western diamond ( <i>C. atrox</i> )....	..	..	23	72	108	15	218
Mojave ( <i>C. s. scutulatus</i> ).....	..	19	10	15	37	66	147
Arizona black ( <i>C. v. cerberus</i> )..	2	3	5	17	..	..	27
Blacktail ( <i>C. m. molossus</i> ).....	..	..	..	5	12	2	19
Speckled ( <i>C. m. pyrrhus</i> ).....	..	..	..	1	11	2	14
Total.....	2	22	38	110	168	85	425

in the Huachucas. The reason for this difference is not yet apparent. For another example: in Arizona, the Mojave rattlesnake (*C. s. scutulatus*) and the western diamond (*C. atrox*) are codenizens of the entire area that either occupies, which constitutes more than half the state—the section lying southwest of the line Clifton-Prescott-Peach Springs. But in California their respective areas are separate, *scutulatus* occupying the Mojave and *atrox* the Colorado Desert. Judging by the ecology of the Arizona territories where they live together, one would have expected either species to thrive in either California desert.

I have already mentioned the difficulty of determining population densities. Relative densities are equally subject to error, as the several species are not equally secretive or conspicuous, and any figures are necessarily dependent on the collecting technique. The following statistics may serve to give at least an indication of relative populations, based on collections made in areas inhabited by more than one species.

From 1926 to 1932, inclusive, section crews along the branch line of the Santa Fe Railway between Ash Fork and Phoenix, Arizona, collected and sent many live rattlesnakes to the San Diego Zoo. In the arid mountain stretch between Ramsgate and Congress Junction, a distance of 50 miles, 5 rattlesnake species occur. The distribution by stations and species is shown in table 8:2.

It will be observed that the only complete overlap is at Hillside, for *cerberus* is rare or absent below this point, and *molossus* and *pyrrhus* above. The latter

pair are rock-dwellers, whereas *atrox* and *scutulatus*, which prefer sandy washes and mesquite thickets, are increasingly prevalent toward the point where the railroad comes out onto the desert plain at Congress Junction.

The following statement, which discusses a similar territory some 60 miles to the east, shows the variations in composite populations that may be observed within a mile:

For ten years, 1918–27, I lived on a homestead one mile south of Montezuma Castle, Arizona, on a river terrace thickly covered with mesquite growth. As a boy, I didn't know the difference between *Crotalus atrox* and *Crotalus scutulatus*, and called them all *atrox*. During that ten years I saw an average of at least a half dozen diamondbacks a year on that flat, and never saw one northern blacktail (*Crotalus m. molossus*). On a hillside across the creek from the flat, during that period, I saw one blacktail. But from 1937 to 1942 at Montezuma Castle, one mile to the north, I saw about as many rattlesnakes a year, and approximately half of these were the blacktails, and the other half *atrox*, save for one *C. s. scutulatus*. Moreover, I saw both common species in identical terrain. Earl Jackson, National Park Service, Las Vegas, Nev.

In the Mojave–Palmdale–Adelanto–Kramer area of the Mojave Desert in California, the Mojave Desert sidewinder (*C. c. cerastes*) and Mojave rattler (*C. s. scutulatus*) occupy the same territory. A record of specimens observed both day and night, and whether alive or dead (run over on the road), showed 131 sidewinders to 78 Mojaves. Similar records in the Borrego area of eastern San Diego County (the Colorado Desert) showed 49 sidewinders, 16 red diamonds, and 2 southwestern speckled rattlers. However, in this latter case the species inhabit different ecological niches; as one proceeds eastward toward the desert, he leaves the red diamond and speckled rattler territory and enters that of the sidewinder, in this case *C. c. laterorepens*.

Chester C. Lamb collected rattlesnakes in the vicinity of La Rivera [= Ribería] in the Cape region of Baja California and secured 13 San Lucan diamonds (*C. r. lucasensis*), 8 Lower California rattlers (*C. e. enyo*), and 3 San Lucan speckled rattlers (*C. m. mitchelli*). Capt. Fred Lewis of the yacht "Stranger," on three separate occasions, had the natives bring in rattlers at Cape San Lucas and obtained the following: 288 specimens of *lucasensis*, 17 of *enyo*, and 62 of *mitchelli*. Although there is little doubt that *lucasensis* is the most common snake in this vicinity, it is probable that Lewis's method of collecting tended to increase the relative numbers of this large and conspicuously colored snake.

The San Diego County statistics, previously cited to show the rattlesnake population as a percentage of the snakes of all kinds, is repeated in table 8:3 in terms of numbers of rattlesnakes to indicate zonal distributions.

Certain zonal preferences are at once evident. It is probable that the foothill area has a really composite population of the three forms *ruber*, *pyrrhus*, and *helleri*; they do not differ greatly in size or in the character of surroundings they prefer, although *pyrrhus* and *ruber* favor rocks, and *ruber* cactus, more than does *helleri*. But they are certainly in competition for food, and I do not doubt that if two were eliminated, the one remaining would soon increase in numbers to the point of replacing the others.

We conclude that certain composite populations of rattlers are only slightly competitive, because of differences in size, prey, or ecological preferences, while

others are fully competitive. Yet I know of no evidence of their obstructing each other in any way or attempting to protect their feeding territories. With respect to denning proclivities, it is to be noted that most composite populations are found in territories where the season of hibernation is so short that individual refuges, rather than extensive dens, are the rule; or they occur in mountain areas where suitable refuges are so close together that the snakes need not travel far to find one. Such meager evidence as is at hand seems to indicate that, in areas inhabited by two or more species, they seek separate winter refuges. This, if it be verified by future observations, would indicate a greater antipathy between rattler

TABLE 8:3  
ZONAL DISTRIBUTION OF A COLLECTION OF RATTLESNAKES FROM SAN DIEGO COUNTY, CALIFORNIA

Subspecies	Zone							Total
	Coast	Inland valleys	Foothills	Moun- tains	Desert foothills	Desert	Zone undeter- mined	
Sidewinder ( <i>C. c. laterorepens</i> ) . . . . .	...	...	...	...	28	123	...	151
Red diamond ( <i>C. r. ruber</i> ) . . . . .	276	354	282	5	84	9	3	1013
Southwestern speckled ( <i>C. m. pyrrhus</i> ) . . . . .	2	51	199	21	52	3	1	329
Southern Pacific ( <i>C. v. helleri</i> ) . . . . .	456	371	273	78	58	...	22	1258
Total . . . . .	734	776	754	104	222	135	26	2751

species than there is between rattlers and harmless snakes, for that the latter often hibernate with the rattlesnakes there is no question (see p. 598).

However, the enmity between rattlesnake species, to whatever extent it exists, is not an active one. I was told by A. Pierce Artran that a southern Pacific and a red diamond rattler were found coiled together two miles east of Laguna Beach, Orange County, California; and at the San Diego Zoo a male southern Pacific mated with a female red diamond and produced hybrid offspring. Recently a *ruber* × *helleri* hybrid was found in the wild. Other hybrids, some involving sympatric species that mated in the wild, whereas others resulted from mating in captivity, have been mentioned elsewhere (p. 239). Captive rattlesnakes of different species, whether of the same or opposite sexes, when caged together at the Zoo have never shown the slightest animosity toward each other. They dwell together in peace, although they may accidentally strike each other in the excitement of being offered food.

Arizona has the greatest number of rattlesnake subspecies (17) within the confines of a single state. It also has the greatest number present at a single point. Charles M. Bogert, in June, 1947, collected *atrox*, *molossus*, *tigris*, and *pyrrhus* at Humbug Gold Mine, 6 miles northwest of Castle Hot Springs, Yavapai County, in one day. It is probable that *cerberus* and *scutulatus* are also to be found in the immediate vicinity, for both have been collected amid similar surroundings only a few miles away.

Areas having several different kinds of rattlers are usually characterized by a rough terrain and a complex vegetation. In such a place appropriate microniches may be found suitable to species normally preferring slightly different habitats; different microclimates may be at hand, with adequate sites for basking; and finally the diverse ecological conditions may produce a diverse food supply.

## HIBERNATING DENS AND THEIR USES

One of the most interesting features of rattlesnake life is their practice of assembling at particular points—dens, they are called—for their winter hibernation. This custom has both habitat and habit aspects; I have elected to discuss it under the former classification. Rattlesnakes are by no means the only snakes that gather into restricted refuges from widespread summer ranges for the purpose of hibernation; yet the great numbers involved and their prominence, as they lie about the den entrances in the last sunny days of autumn or first warm days of spring—which I have termed the “lying-out” periods—have resulted in a marked focus of attention on the practice.

These denning proclivities are more conspicuous in northern areas, or at higher altitudes, for here fully protective refuges are more necessary and population concentrations are greater. In the south, where a shorter season of hibernation prevails, or where it may even be interrupted by occasional warm spells, the snakes take advantage of any convenient hole or rock crevice. In these more makeshift situations only a few rattlers may gather together for the winter; or they may even seek separate shelters.

Although rattlesnake hibernation is a period of inactivity, at the time when they are gathering for hibernation rattlesnakes are much more in evidence than during their season of activity, and more is known of their behavior about their dens than on their summer ranges. For this reason I shall discuss denning in advance of summer activity. Of the rattlers that do use regular dens, the western rattlesnakes (*C. viridis*), particularly the subspecies defined as the prairie rattlesnake (*C. v. viridis*), the Great Basin rattler (*C. v. lutosus*), and the northern Pacific rattler (*C. v. oreganus*), have the best-known denning habits, and the observations made by my correspondents mostly refer to these subspecies, although the timber rattlesnake (*C. h. horridus*) is also mentioned in some detail.

### PHYSICAL CHARACTER OF DENS

In a discussion first of the physical character of the dens, it is to be noted that, where rocky formations are available, the snakes seek deep caverns or crevices; but in the plains areas they are forced to use the holes of mammals, particularly those of the gregarious prairie dogs.

The degree of cold reached in any area not only affects the duration of hibernation but also the nature—the depth, particularly—of the refuge. Thus, in mild climates a snake may be rendered immobile by torpor, should the temperature fall to 40° F. (4.7° C.) or thereabouts, for which reason it must have a protective retreat while in this defenseless condition. But it need not fear death by freezing as in a more rigorous climate, where the refuge must be below the frost line.

*Prairie Rattlesnake* (*C. v. viridis*).—The characteristics which a den must have to afford adequate protection to the hibernating snakes of this subspecies have been outlined by A. M. Jackley, who, in the course of his snake-control work in South Dakota, located many dens of the prairie rattlesnake (*C. v. viridis*) and observed the habits of the rattlers in using them:

Fully 90 per cent of the maturer rattlers congregate annually in groups of from 50<sup>1</sup> to several hundred to hibernate in the same den. I think about 250 is the average number hibernating together, though I know of several times this number using some dens. The first frost starts them toward their winter refuge. Slowly but surely they find their way back. The old snakes seem to lead the way and the young ones, that is, the one- and two-year-olds, follow their trails. I have watched them coming to their dens for hours. It is my opinion that the majority of the young-of-the-year do not go to the dens, except where the older snakes hibernate in prairie-dog towns. I think these little ones seek ground holes and similar places of refuge. In fact, I occasionally find that even adult stragglers survive the winter in small burrows, such as are dug by the striped gopher.

There are two requirements essential for a den, depth and dryness. Snakes hibernate only in places that are not subject to floods, and in dens penetrating to a depth below the frost line. They must find such holes or cavities as nature provides. Prairie dogs and badgers are the only burrowing animals that dig deep enough holes; consequently on the open prairie many groups hibernate in dog towns. In more irregular or rocky areas, the best accommodations are offered by slides on steep bluffs, cracked-open banks along deep gullies, sinkholes or washouts that have ceased to conduct water, crevices in rock ledges, caves, or porous scoria deposits.

It is conservative to say that 90 per cent of the dens are protected from the north wind, that is to say, they are on the southern slopes of the bluffs. Even in prairie-dog towns, the holes are selected that are especially favored by the warm sun. Most of the large colonies occupy dens in the rough areas and near the tops of high ridges or buttes [fig. 8:2].

Where the soil is light and subject to drift, dens are likely to be more or less temporary, for rattlers do not keep the galleries cleared as would the original prairie-dog occupants. Prairie-dog holes extend for 50 feet or more, and go down to a depth of 10 to 12 feet. The holes at a den are rounded out and worn slick by frequent entry, and any one with experience will readily recognize a den.

When prairie dogs abandon a town to rattlers, the burrows gradually fill up. Eventually they must be abandoned for new localities. Rattlers normally select the burrows that are at slight elevations, on southern slopes and well protected from flood waters. They usually take over a small section of a dog town and occupy the same holes as long as they are tenable. Then they take possession of other burrows and force the dogs to withdraw and dig new holes, and so on.

C. B. Perkins has thus described certain dens where a large collection of prairie rattlesnakes were secured:

During the summer we had spotted three prairie-dog towns, two of large size, and hoped to be lucky enough to be there for "home-coming week." These dog towns are located about 10 miles due east of Platteville, Colorado, near Milton Reservoir, in what are called the Sand Hills, about 50 miles northeast of Denver. Low growths of sage brush are plentiful and so is buffalo grass; there are yuccas, tumbleweed, prickly pear, and some member of the pigweed family which grows to a ball about a foot in diameter, and in November turns a glorious purple-red. Town No. 1 in which we got the most rattlers, is in a cattle-grazing area. We saw no cattle in the town itself, although there were occasional droppings, and very little vegetation and no sage brush. Town No. 1 covers about 120 acres; No. 2, 20 acres; and No. 3, 300 acres, although it proved the poorest town. Town No. 3 is 2 miles south of town No. 1, and town No. 2 about 1 mile south of town No. 3.

The following are some additional notes from my correspondents on prairie-rattler dens:

My experience has been that prairie rattlesnakes make for some high rocky hill late in the fall, where instinct or memory tells them there is a suitable place to hole up, preferably where the rocks are loose and there are many crevices to crawl into. Such a den is usually right on top of a high hill or mountain. Just how deep they go, I cannot say. Some years ago, a group of men tried digging out a den in this locality but never did get down to where the snakes had holed up for the winter. They dug down for six or eight feet, but the rocks became too solid to work in any farther, although they were still full of crevices. *J. Fred Toman, Bowers, Mont.*



One place where the rattlers find conditions suitable for denning is in prairie-dog towns. To dig deep enough to winter, the prairie dogs must have fairly stable soil. Their holes would cave in if dug in the sand. They find a few flats not far from the streams where there is sufficient clay to make firm soil; at least, these are the only sites where their towns can be found, and every town is a potential snake den. *Charles W. Stavely, U. S. Forest Service, Nenzel, Nebr.*



The rattlers in this area usually select dens on rocky south slopes, especially in the timber. In the open country they select old abandoned rodent holes or burrows. *George S. Gorsuch, U. S. Forest Service, Wheatland, Wyo.*



The rattlesnake dens here usually consist of cave openings in limestone cliffs. These caves are on dry sunny exposures from 100 to 300 feet above the valley floors. *K. J. Helmick, U. S. Forest Service, Nemo, S. Dak.*

Published descriptions of prairie-rattlesnake dens will be found in David (1937, p. 265), Gloyd (1946, p. 87), Anderson (1947, p. 1), Murphree (1948, p. 17), and Sweet (1954, p. 54).

*Great Basin Rattlesnake* (*C. v. lutosus*).—Dens frequented by the Great Basin rattlers are much the same as those of the prairie rattlers, except that, because of the usual availability of rockslides, they have to seek mammal holes less frequently than do the prairie rattlers.

One good-sized den is located on the desert lands at the northwest corner of Great Salt Lake near Locomotive Springs. The formation here is of a volcanic nature and there are several other dens in a number of places round about. *Lee Kay, Utah Fish and Game Commission, Salt Lake City, Utah.*

E. R. Hall (1929, p. 79) has described a *lutosus* den in eastern Nevada:

The den is a hole about 10 feet deep and approximately 15 feet in diameter at the north end of a red butte which stands out as the only irregularity visible for several miles on the otherwise level, non-rocky valley floor. . . . This butte, about 50 feet high, one-fourth of a mile long and one-sixth of a mile wide, is composed of volcanic boulders. The interstices of this volcanic intrusion now are mostly filled with wind-blown soil. However, crevices of undetermined extent can be found, and it probably was one or several of these which the rattlesnakes used as a den. [The den was visited by Hall after the rattlers had emerged and were lying about under rocks and bushes.]

Woodbury (1951, p. 4) thus describes the places used as dens by the Great Basin rattlesnake (*C. v. lutosus*) and by the midget faded rattlesnake (*C. v. decolor*):

Experience in hunting snake dens in Utah and western Colorado indicates that snakes do not make their own hibernating burrows but depend upon finding suitable places. They

have been observed in loose cobblestone rocks, in gravel banks, in lava beds, in dry spring channels, in rock crevices and in artificial hibernating places such as garbage dumps, rock walls and open house foundations. [Probably some of these types of refuge refer to those used by snakes other than rattlesnakes.]

Woodbury and Hansen (1950, p. 66) tested the rock fissures at a *C. v. lutosus* den and found, by probing with a wire, that some of the cracks penetrated at least 15 feet.

*Northern Pacific Rattlesnake* (*C. v. oregonus*).—Paul J. Martin sent me the following account of dens in rocky territory near Pateros, Okanogan County, Washington, where he collected a large series of northern Pacific rattlesnakes:

Some years back I made the acquaintance of the owner of an orchard tract in the vicinity of Pateros. I learned that he had two or three rattlesnake dens on his premises. His orchard land is located on what appears to be an old river flat, and rising up from this flat is a low range of mountainous country, extremely steep and varying from slide-rock to huge boulders of hundreds of tons. Great crevices and faults occur in this steep hillside, and it is here that we found the dens. They were located perhaps 300 to 500 feet up from the riverbed, the snakes in hibernating apparently seeking the most arid locations. Altogether, over an area of perhaps 10 acres of this hillside, we found 7 or 8 dens; and each year over a period of two weeks they yielded on the average about 350 to 400 rattlers. These were by no means the only dens in this immediate section of the country. Within a radius of 5 to 7 miles there were at least 15 dens. Naturally, in view of the fact that we have now hunted for years on this property, the snakes are not so numerous as a few years ago. However, I should say that there are plenty still to be had, and no trouble should be experienced in capturing 300 or 400 over a short period during a spring season.

In my travels through the Northwest, I have found no other place where the rattlesnakes and their dens are in evidence in such numbers. This country is rather remote from civilization; and further, in view of the fact that there are no through paved highways and less traffic than in the average section, I should say that these conditions account in part for the great numbers of snakes. Wild life is always forced back by population and cultivation, and I assume that reptilian life would be no exception.

Of the dens I have visited, I have never found one in a location other than on a south slope, the reason for this being obvious. In my experience the snakes' emergence from hibernation in the spring is regulated according to the season. Sometimes this country gets a heavy snowfall and hard winters; other years there is scarcely any winter at all, which naturally is followed by an early spring.

A. C. Mackie thus describes the dens which he has often raided in the vicinity of Vernon, British Columbia, dens that are also in rocky territories:

Generally speaking, snakes prefer to den up as near to the summit as possible, for such positions are more exposed to the sun and allow the occupants to spread to all points of the compass for the summer. Where, however, the summit-rocks are not pervious they are forced to choose isolated outcroppings, well supplied with fissures, at lower elevations. The dens almost invariably have a southern aspect and must be deep, dry, and free from risk of seepage. How deep is hard to say, but the blasting of one den disclosed no signs of the dormitory proper, nor were any snakes subsequently found to have been injured by the blast; probably 8 to 10 feet would be a fair average depth. The dens generally occupy an exposed position but the subsequent growth of brush, trees, etc., may appear to contradict this. In one case at least, the original den, situated at the base of a granite cliff, has been overlain by a slide of small stones from a nearby rock-chimney, so that no one would suspect its existence. The snakes are forced to descend an 8-foot overlay of broken rock before reaching the original opening to their den.

They occasionally hibernate in a rockslide, if the neighboring rocks are devoid of crevices. Such a condition exists on the west side of Vaseau Lake in the south Okanogan Valley

where the neighboring cliff is impervious and a narrow cleft is choked with boulders, some of which weigh several tons and give adequate depth and shelter. The slide faces north, as does another isolated den on a bluff to the west. Such an aspect is due to the fact that the exposed rocks all face north. Snakes must therefore choose dens alien to their preference and in consequence emerge rather later than their confreres at the north end of the valley. A favorite den-site is at or near the head of a rockslide. This is because the rock is obviously soft and pervious; in such cases the snakes have probably receded farther and farther into the rock as portions have become detached from its face.

During the years 1930-34 I confined my activities to the hill about one mile due south of our school, on the south face of which were two dens from which snakes had been killed for several years previously. The approach to this hill is a steadily rising slope covered with bunch grass, but the southern face is everywhere steep and in some sections precipitous. The vegetation is sparse. Conifers are fairly well distributed. This mile-long face has at least five dens.

The chance discovery of a den on this hill in 1934 diverted my energies more and more to this area, and resulted in the finding of about a dozen dens and as many lodges. These latter differ from dens in the lesser numbers of their occupants and may result from a few snakes being overtaken by cold weather before they can reach their winter-quarters, or to overcrowding in a den and the consequent necessity of founding a new colony.

Other notes on northern Pacific rattlesnake dens are as follows:

I have found many rattlesnake dens and have dug out several. They are in rockslides and shale rock, on the south exposures of the canyons. *Jesse L. Harris, Government Hunter, Pilot Rock, Oreg.*



What few rattler dens I have found have been below rock bluffs where the loose rock affords protection. We have found the largest dens in among the bluffs where they are able to get into crevices. *L. J. Cooper, U. S. Forest Service, Merlin, Oreg.*



Near Pleasant Valley, in the northern part of Yosemite Park, there is a den of rattlesnakes. Here there is a mountain with much exfoliated granite, and beneath these exfoliations the snakes winter in numbers. I walked up that way one morning and saw many snakes out on the little ledges and watched them go back in as I came by, and heard them rattling underneath as I walked over the dens. *Albert C. Hawbecker, Madera, Calif.*

Fitch and Glading (1947, pp. 106, 121) and Fitch (1949a, p. 544) have shown that the northern Pacific rattlesnakes (*C. v. oregonus*) in the milder climate at the San Joaquin Experimental Range in Madera County, California, take refuge singly or in small groups under boulders and in mammal burrows, rather than in large aggregations, as in the more rigorous climate to the north or at higher elevations. However, W. E. Howard has lately cited evidence indicating the presence of several real dens in the vicinity of the Range.

*Timber Rattlesnake* (*C. h. horridus*).—A rattlesnake, other than *C. viridis* and its subspecies, required by a severe winter climate to seek well-protected places for hibernation sites, is the timber rattlesnake. It usually selects a rocky den with a south exposure (Netting, 1932, p. 13; McCauley, 1945, p. 137; Anderson, 1951, p. 7).

Stephen H. Harwig of Pittsburgh has had much experience resulting from an intensive study of *horridus* and its denning habits in western Pennsylvania. He has this to say about the character of the dens in that area:

In a 1,000-foot ledge, there may be two or three main snake areas, at one or both ends and in the middle. Such areas usually entail one or more large stone slabs, from 3 to 10

feet in diameter, and 6 to 20 inches thick, which may be thought of as "key" rocks or "den" rocks. The slabs, for the best conditions, must be in a dry, sunny location, must have 1 to 3 inches of clearance below, and with huckleberry bushes growing along one or more sides. The snakes sun themselves in moderate weather by lying under the partial shade of the bushes, usually within a foot or so of sanctuary under the rock. The actual winter refuges may be vertical fissures under a den rock, or the vertical fissures that comprise the entrances to the true dens may be distant as much as 40 feet from the den rock. The den rock affords quickly accessible refuges during the season when the snakes are taking advantage of the last warm days of fall or the first of spring; but it provides safety from enemies, not cold, from which the snakes must seek the protection of the deep vertical fissures that are the entrances to their winter-long hiding places.

A long ledge may have from 1 to 5 den rocks, widely separated, yet I should call the whole ledge one den. The preferred ledges face southwest, but many face southeast, south, or west. Some dens are composed of sliderocks rather than ledges; they lie nearer the streams, on the slopes of the hills below the ledges. They generally consist of jumbled piles of relatively small rocks, say 1 to 2 feet in diameter, but there will usually be 2 or 3 key rocks, 3 to 10 feet in diameter nearby.

Dens of *C. h. horridus* in western Pennsylvania are all different, yet the same in many ways. One type is sandstone, with little or no conglomerate; a broken, fissured ledge, involving a 10- to 30-foot drop on the downhill side, and with the upper side grading into the hilltop, which is about level back of the ledge. The ledge may be 3 to 50 feet in width, usually about 15 feet. It may be only 200 feet long, but is more often about 600 feet, and rarely a mile or even more. The rattlesnakes are found on the level top of the ledge, and on the adjoining ground 1 to 10 feet from the ledge top, and on jumbled rock slides below the ledge. There are numerous slab rocks, cleaved slabs of sandstone, either entirely separate from the underlying ledge, or undercut by erosion on several sides. Snakes are found beside or under, and rarely on top of these slabs, which may vary from 24 by 30 inches and 3 inches thick, up to 30 by 30 feet and 18 inches thick. A good ledge usually parallels a stream, but is not near the stream; rather, it is high on a ridge dividing two streams. The ridge may be from 200 to 3,000 feet wide at the top, which is rarely more than 10 to 30 feet higher than the ledge. The ledge-top is exposed and sunny in some places, but in others shaded by trees or dense shrubbery. The shaded-over places are no good for snakes.

Several collectors have observed that rattlers may be found denning in one rocky place, but will be absent in another nearby that has the same superficial characteristics. It is to be assumed that there are differences below ground, one having adequate fissures free from moisture and drafts, and penetrating well below the frost line, whereas the others are not so favored. Harwig had this to say about the depth at which rattlers hibernate in western Pennsylvania:

I have no facts on depth of hibernation, but believe the refuges go down through 3 to 20 feet of porous fragmented rock or crevices, to where the fissures merge with more and more earth. The earth is probably sandy, mixed with the leaves and twig debris of several years. The snakes should find frost-free pockets only 3 to 8 feet within such sandy, leafy crevices, at a total depth of from 6 to 30 feet below the surface, if the initial fissures be included. At such depths, sealed in by snow and ice, the snakes should remain above 32° F. all winter. But still I think there must occasionally occur a severe winter kill, especially among rattlers that seek individual refuges under slab piles, stumps, and deserted buildings. Even dens may deteriorate, or may in some years be inadequately sealed because of some quirk in the weather, with fatal results to most of the inmates.

In parts of New Jersey, where rocky areas are not available, *horridus* is known to take refuge in sphagnum-moss bogs, a fact noted as early as 1799 by Beauvois (p. 373; also Daudin, 1801-4, vol. 5, p. 298). More recent descriptions of such refuges are those of Scoville (1929, p. 56), Burger (1934, p. 142), and Conniff,

(1948, p. 49). The snakes are said to go into moss or into holes in sand to a depth of 1½ to 2 feet. The moss may be cut and rolled back like a rug, uncovering the rattlers beneath. Sometimes they are partly in water.

Miller (1938, p. 17) has reported that the massasaugas (*S. c. catenatus*) in western Pennsylvania hibernate in natural fissures, animal burrows, under heavy moss, or under overturned trees. Many other reports from my correspondents give an essentially similar picture of the physical character of the localities selected as dens in northern areas with severe winters—fissured cliffs or rockslides with southern exposures, and high enough on the slopes to be well drained; and, where rock formations are not available, mammal galleries, moss, or plant debris.

*Eastern Diamondback* (*C. adamanteus*).—In more southerly areas, with winters less severe, aggregations of rattlesnakes are smaller; and individuals may seek seclusion alone, in whatever hiding places they come upon. The following observations apply to the eastern diamondback rattler, to whatever extent this species finds it necessary to seek dens in the relatively mild climate to which it is subjected:

In the region between Thomasville, Georgia, and Tallahassee, Florida, the diamondbacks commonly den in holes beneath the bases of wind-blown trees, holes left by rotted pine stumps, or in holes dug by the gopher tortoise. Two or three is the largest number I ever heard of being found together. *Charles O. Handley, Fish and Wildlife Service, Blacksburg, Va.*



Diamondbacks prefer rocky country for dens, but there is little of this in Florida, so they use land-tortoise holes. They are also found in palmetto thickets under logs. *Joseph T. McCullough, U. S. Forest Service, Brooklyn, Miss.*



Rattlers like to bed down for the winter in old logs or stumps. I have never found more than one at a place. *J. Lawton Huggins, Game Warden, Mullins, S. C.*

Robert E. Gordon, of Atlanta, Georgia, wrote that *adamanteus* wintered under stumps. Professional hunters were said to push these over with bulldozers, and to have found as many as 15 to 25 rattlers under a single stump. Ariza (1948, p. 61) says that a harrican—the big hole left where the wind has blown over a tree—is a favorite hibernation site for diamondbacks. Wilfred T. Neill informed me that eastern diamondbacks congregate to some extent in Florida. Several may seek refuge in a single gopher-tortoise hole, with others in nearby holes round about.

*Western Diamondback* (*C. atrox*).—Dens of rattlesnakes in the Southwest are much the same in character as those in the Northwest, except that the concentration of snakes is usually less. The following statements largely refer to the western diamond rattlesnake (*C. atrox*), although other species are found in the same areas, and probably hibernate in similar situations:

I found one den located on the south side of a mountain, on an 18-foot cliff of solid rock, up and down, with the entrance at the base. I judge that there were possibly 200 rattlesnakes at this den. Of course, as soon as the shooting started, the snakes began to make for the den in the rocks. After some fifteen minutes we could see no movements of other snakes. We went down and gathered up our kill, some extra large ones measuring 5 to 6½ feet, with up to 12 rattles. We had killed 18. *Clyde Burleson, Byron, Okla.*

One fall in the early 30's, some road construction machinery dug up rattlesnakes about 10 miles east of Bishop, Nueces County, Texas. Great cracks had formed in the heavy black soil during a dry summer, and the reptiles had apparently crawled down into the cracks for winter dens. One such assembly was reported to consist of more than 100 snakes. W. C. Glazener, *Wildlife Biologist, Falfurrias, Tex.*



There is a snake den within two miles of Archer City, Texas, or there was in 1918, where I killed rattlers on warm days in the winter. The highest number killed on one day was 9. The opening of this cave was large enough to walk in, but the general formation was a flat crevice from 2 to 6 or 8 inches high and 12 feet long. William T. Sherman, *Silver City, N. Mex.*



Rattlers are seldom seen during the cold winter months, but I once found a bunch of 8 in a small cave in February at an elevation of about 3,000 feet. They were sluggish and stiff but able to travel slowly. This cave was in a dirt bank about 10 feet above the bottom of a dry wash. The den was about 6 inches in diameter at the opening. Clyde P. Moose, *U. S. Forest Service, Cavecreek, Ariz.*

Dobie (1946a, p. 12) remarked that in the Texas plains the rattlers do not gather in large dens; rather they scatter into badger holes, rats' nests, and similar refuges.

*Southern California Rattlesnakes.*—In the mild climate of southern California, although rattlers are rarely seen in winter, their dens are only impromptu refuges, such as mammal holes, shallow rock crevices, or piles of leaves. The rattlers often take advantage of a warm spell at any time during winter to come out for a few hours to sun themselves. In consequence, the concentration of numbers is nothing like that found in colder climates. But at higher elevations, where the winter is more severe, the dens are more like those found in the North and East.

One of the greatest concentrations of which I have heard in San Diego County comprised about 20 speckled rattlers (*C. m. pyrrhus*) in a horizontal cleft of a granite boulder near Ramona. These snakes were found by Louis P. Faldborg on November 11, and were in so deep they could not be reached, although he could see them. He returned November 25, but they were farther in; they could be heard but only one could be seen.

Other reports are usually of single rattlers or pairs found under rocks, in deep crevices, or down mammal holes. A southern Pacific rattler (*C. v. helleri*) was found hibernating at La Jolla, in January, under only a 3- or 4-inch cover of leaves. Walter T. Pew of Hemet reported: "Digging out a bee cave in the rocks one winter, I found a pair of large rattlesnakes that had holed up next to the bees, I suppose for warmth."

Occasionally it has been said that rattlesnakes dig the holes they use as dens. Among others having this belief was Kalm (1752–53, p. 313; 1758, p. 287). This is probably never true. Where suitable rock formations are not available, they depend on mammal burrows or on masses of vegetation of some kind. The fact that prairie rattlers must abandon prairie-dog holes after a time, since they cannot properly maintain them, is well known. The rattler's snout is poorly formed for digging, compared to those of many other kinds of snakes, some of which have sharp snouts and are expert burrowers. Hopkins (1905, p. 354) reports having plugged a hole containing a western diamond rattler. When he

returned two days later he found that the snake had smashed its nose and blinded itself trying to get out.

Tome (1928, p. 115, but written in 1854) thought that rattlesnakes couldn't turn in a hole or back out, and hence must always dig their way out, a quite fantastic idea, and a dangerous one as well; for a rattler may turn in a hole and have its head watching the entrance while the tail is still crawling in, so that anyone grabbing the tail is in danger of being bitten.

#### DEN POPULATIONS

The number of rattlesnakes inhabiting a den depends on topography and climate. Where suitable sites are widely separated, populations at specific dens tend to run larger; but where adequate rock slides and crevices are numerous the snakes do not congregate from such distant points. Yet even where good refuges are close together, the gregarious nature of the snakes will lead to the selection of particular sites so that the concentrations are fairly large. It is only along the southern border of the United States, where the season of hibernation is quite short, that the selection of a refuge becomes more a matter of individual than group choice.

The several subspecies of the western rattlesnake (*C. viridis*), especially in the northern parts of their ranges, undoubtedly attain the greatest den concentrations. A. M. Jackley's statement that dens of the prairie rattlesnake (*C. v. viridis*) in South Dakota contain from 50 to several hundred inmates, with an average of about 250, has already been quoted. Other data on den populations of this subspecies supplied by my correspondents are as follows:

I helped to kill 125 rattlesnakes in two dens, this last summer. *Harry Henderson, Buffalo, S. Dak.*



We have found in the spring hundreds of rattlers congregated at Eagle Canyon; also in southwestern Keith County. *Ed Sudman, Ogallala, Nebr.*



In the next day or so, I am expressing to you 152 prairie rattlesnakes. We found three prairie-dog towns and watched them all summer. We hit the right day—93 one day, and the rest the day before and the day after (October 12, 13, 14). I'm sorry that so many are small. More than 50, however, are as large as we usually see. All these are from the neighborhood of Milton reservoir, 10 miles east of Platteville, Colorado. *C. B. Perkins, then of Denver, Colo.*

Floyd M. Hunsaker, of Pueblo, Colorado, with several associates, in four days killed 485 rattlers at a one-acre prairie-dog den 30 miles northeast of Olney Springs, Colorado, in the autumn of 1937. This exploit was publicized throughout the country, illustrated by pictures of the dead snakes (e. g., MacClary, 1939a, p. 12). My inquiry concerning the number of snakes at the den brought the following reply:

We accidentally found the snakes on almost bare ground that contained probably 30 prairie-dog holes. They were at the height of their migration to these holes to hibernate, as they were coming in from all directions except the east. We certainly were lucky that no one was bitten with so many snakes around.

We have made several trips back since the day we made the big kill and have gotten some snakes each time. Every time we left we thought we had killed them all. On the last

few visits we have been catching them alive. We have about 80, in sizes from 10 inches to about 45 inches; but if we had started to catch them alive when we first found them we could have got over 300 that would run over 40 inches, to say nothing of the young ones.

A week after Hunsaker's big catch, other hunters got 208 rattlers at the same prairie-dog town. Other data on the populations of *viridis* dens are the following:

The number of prairie rattlesnakes in a den may range from singles and pairs to as many as 450 in an area of less than 5 acres. The largest concentration I have seen was on a rocky ridge 50 miles south and west of Gillette, Wyoming, some 15 years ago; they were gathering from all points of the compass to their denning location, which I did not trouble to locate exactly. I killed snakes with my rifle, until I ran out of shells; then with rocks, until my arm wore out, and still left many for seed.

I was marking timber on a rocky ridge of sliding slate-rock in Rapid Creek Canyon in 1922 in April, when a pair of log cutters felled a tree near me. The stump pulled out and opened a den containing at least 100 buzzing snakes. With so much convenient cover, many of them got away and, though three of us accounted for 55, we left many singing away under nearby rocks. *F. R. Cochran, U. S. Forest Service, Sundance, Wyo.*



Rattlers are found in dens in groups of 50 to 200, at an average depth of 3 feet. Most snakes summer in grassy areas of the badlands along the Missouri River; but the dens are in rocky areas. *C. W. Griffin, Glasgow, Mont.*



As a boy, I spent many of my summer vacations at my uncle's cattle range on Sixteen Mile Creek, approximately 45 miles from Bozeman, Montana. The bottomland and the foothills along the creek were infested with prairie rattlers. In cuts along the old Jaw Bone Railroad, which ran through the Baker Ranch between Harlowton and Lombard, Montana, I have seen on a sunny afternoon as many as 100 rattlesnakes coiled up on the rocks, having their dens in crevices created from blasting cuts through the hills. *W. G. Willson, Los Angeles, Calif.*



Rattlers den up for the winter sometimes in groups of as many as 150 snakes or more. *T. V. Pearson, U. S. Forest Service, Salmon, Idaho.*

Keim (1870, p. 271) reported raiding a prairie rattler den where more than 200 had been killed; he counted the remains of 158. Sweet (1954, p. 55) stated that an average raid in Montana in the spring would produce from 30 to 50 rattlers. Some other reports of den concentrations of prairie rattlers will be found on p. 530.

The following notes apply to the Great Basin rattler (*C. v. lutosus*):

There is a place above Sweet where a woman killed 148 rattlesnakes once, as they were coming out in spring. *Bill Talley, Sweet, Idaho.*



Some very large dens of rattlers have been located near here. About 600 were taken out of one den, which was just a starter. *Joe Garner, Shoshone, Idaho.*



Most rattlesnake dens are found in rocks, where they get down into crevices, sometimes in large numbers. I have taken 50 rattlesnakes out of one rocky hole. *Merrill Nielson, U. S. Forest Service, Spanish Fork, Utah.*



I have seen three or four hundred rattlers denning in one rock ledge. *Lawrence Kelly, Harper, Oreg.*

Hall (1929, p. 80) reported that 139 specimens of *lutosus* were killed at a den in eastern Nevada in a single day. Woodbury and Hansen (1950, p. 66) men-

tion a den in Juab County, Utah, where an estimated 300 rattlers were killed. Some years later the authors caught 69 rattlers at this den during the fall gathering. Another den near Grantsville, Tooele County, Utah, was kept under observation for 10 years, during which time 930 rattlesnakes were recorded as being tenants for one or more winters.

The denning proclivities of the northern Pacific rattlesnakes (*C. v. oreganus*) are well known. The numbers at single dens are only slightly below those of the prairie rattler.

There is one cave in the Grand Dalles district where about 100 rattlesnakes have been taken out most every year. *C. L. Winters, Goldendale, Wash.*



In British Columbia, the Pacific rattlesnakes generally den up in large groups numbering from perhaps 50 to several hundred. *A. C. Mackie, Vernon, B. C.*

P. J. Martin (1930, p. 77) has described the capture of over 200 Pacific rattlesnakes at a series of dens in Okanogan County, Washington. Subsequent to the appearance of that publication he sent me several very large series from the same dens. From one group of dens he obtained from 350 to 400 snakes each season. Another collector informed me that, although most dens in this area contained from 200 to 300 rattlers, he believed that some exceeded 1,000.

These many statements indicate that the several subspecies of the western rattlesnake (*C. viridis*) undoubtedly gather at dens in numbers well into the hundreds. Thousands have been occasionally reported, but seemingly not based on careful counts, so a further verification of such large numbers is desirable. One such statement is from Wyoming, where the subspecies is *C. v. viridis*:

The largest den of rattlers that I have helped destroy had, I will say, more than 3,500. I have heard of dens where five or six thousand were killed. I do not doubt the killing of this number in a single den.

Another correspondent from Washington (where the subspecies is *C. v. oreganus*) writes:

I have found many rattlesnake dens in my travels and hikes in the hills. I caught over 1,000 rattlers in one den not far from here.

In the East, the timber rattlesnake (*C. h. horridus*) concentrates in somewhat smaller numbers:

Rattler dens are usually in rough and rocky places, generally with an eastern exposure. I have taken 128 live snakes out of one den in a single day, and a number of others got away. *Frank E. Brink, Fish Warden, Milford, Pa.*



I have reasonably authentic information to the effect that 70 rattlesnakes were killed at one time near the mouth of a rock den located on Fox Tree, a tributary of the Cranberry River, about 8 miles east of Richwood, West Virginia. *C. R. Carr, U. S. Forest Service, Richwood, W. Va.*



I know of one instance on the Pisgah National Forest, in which a total of 30 adult rattlers and copperheads were killed at one time by the dynamiting of a den. *John H. Stanley, U. S. Forest Service, Andrews, N. C.*

Surface (1906, p. 195) reported the killing of 250 timber rattlers within a week at a den in Franklin County, Pennsylvania. Stephen H. Harwig estimates the den populations in western Pennsylvania at from 20 to 200 rattlers. Wheatley (1886, p. 523) reported that several people killed 486 rattlers issuing from hibernation in Trumbull County, Ohio, on May 1, 1799. It is not stated whether more than one den was involved. Russ (1950, p. 47) mentions large numbers killed in Elk County, Pennsylvania.

Neill (1948, p. 113) found only one canebrake rattler (*C. h. atricaudatus*) hibernating singly whereas others were grouped, and therefore concluded that gathering in dens is characteristic of this southern subspecies. Allen and Neill (1950c, p. 35) recorded 81 in one den.

As I have said, in the southern part of the United States, less populous dens seem to be the rule, although the gregarious habit is still evident. A few reports mention snakes in excess of 100 to a den. I have such records of dens of the western diamond rattler (*C. atrox*); the Panamint rattler (*C. m. stephensi*), one of which was reputed to contain 180 snakes and another 104; the speckled rattler (*C. m. pyrrhus*); and the Arizona prairie rattler (*C. v. nuntius*), one den of the latter having 121 inmates. I have already mentioned the report of about 20 speckled rattlers in a rock cleft in San Diego County; on another occasion 9 were found under a rock. In 1932 it was reported that 24 red diamond rattlesnakes (*C. r. ruber*) were blasted out of a rock crevice at El Monte Park, San Diego County, in the course of road construction.

The following is a report on several western diamond rattler (*C. atrox*) dens:

Thirty-seven rattlesnakes is the most I ever found in one den. These were small snakes. I captured 11 rattlers that weighed 55 pounds at one den on the Martin Ranch, Mason County, Texas. At one den on the same ranch I captured 21 snakes that weighed a total of 35 pounds. Most of the dens I have found had less than 20 snakes to the den. *J. D. Bankston, Mason, Tex.*

Some published accounts, not previously mentioned, of the numbers of rattlers found at dens are the following: J. Green (1821, p. 85), G. W. Kendall (1844, vol. 1, p. 160), Yarrow and Henshaw (1878, p. 1633), Matteson (1899, p. 668), Chittenden (1903, p. 47), Morse (1927, p. 217), Motl (1936, p. 7), Anon. (1937, p. 207), and Anderson (1947, p. 1).

Summer aggregations of snakes have been discussed by Noble and Clausen (1936, p. 271). There have been unverified reports of large summer concentrations of rattlesnakes, particularly of *C. h. horridus*.

#### DIMINUTION THROUGH RAIDING

When dens are repeatedly raided year after year, a reduction in the number of occupants is usually evident, although the complete extermination of a colony seems rarely to be effected. A. M. Jackley's control activities in South Dakota showed definitely that rattlesnake populations were decreased at the dens that he, and the farmers and stock raisers under his direction, raided periodically.

A. C. Mackie of Vernon, British Columbia, is the only one of my correspondents who has kept a record of his collections at several dens of the northern Pacific rattlesnake. He writes:

The southern face of the hill where the *oreganus* dens are located is steep. There is a mile-long face which has at least six dens which I have named after those who first discovered them or after some local feature. The appended table [table 8:4] shows the bags made to date:

TABLE 8:4  
ANNUAL CATCHES AT SEVERAL DENS OF THE NORTHERN PACIFIC  
RATTLESNAKE IN BRITISH COLUMBIA

Year	<i>Paternoster</i>	<i>Leech</i>	<i>Austen</i>	<i>Whittall</i>	<i>Poopdeck</i>	<i>Passim</i>	Total
1930.....	..	34	..	55	..	..	89
1931.....	..	12	..	14	..	..	26
1932.....	..	19	..	23	..	..	42
1933.....	..	4	..	27	..	..	31
1934.....	..	0	..	16	..	..	16
1935.....	..	0	12	0	..	4	16
1936.....	..	?	?	?	..	?	?
1937.....	..	0	0	0	..	0	0
1938.....	13	1	6	3	..	0	23
1939.....	14	0	9	7	..	0	30
1940.....	1	1	2	1	8	2	15
1941.....	3	0	4	6	12	3	28
1942.....	0	0	1	5	1	5	12
1943.....	0	0	1	1	3	7	12
1944.....	0	0	1	0	2	5	8
1945.....	0	0	3	0	9	0	12
1946.....	1	1	4	0	5	2	13
1947.....	0	0	0	3	1	0	4
1948.....	0	0	0	0	1	0	1
1949.....	1	0	0	4	1	0	6
1950.....	0	0	0	3	3	0	6
1951.....	0	0	0	1	1	2	4
1952.....	0	0	0	3	2	2	7
1953.....	1	0	0	2	0	5	8
Total.....	34	72	43	174	49	37	409

In table 8:4 I have listed only the earliest-discovered dens that Mr. Mackie has raided. Subsequently, as the take from these declined, he widened his area of operations, with the discovery of many new dens. Altogether he accounted for the destruction of 2,918 rattlesnakes in the years 1930 to 1953, inclusive. But each individual den has shown a progressive decline over the years, indicating that, with continued persecution, the dens do not become repopulated with their original numbers. Always the newly discovered dens have proved the most fruitful.

Woodbury and Hansen (1950, p. 68) reported that a den of Great Basin rattlers that had been raided and 300 killed by sheepherders and construction workers in 1937, had not recovered 12 years later. Sweet (1954, p. 110) thought that his raids on dens of the prairie rattlesnake in Montana had not reduced the successive catches, but most of his raids were limited to a single spring day at each den. More persistent hunting would unquestionably have had a more evident effect.

Elsewhere (pp. 1006 and 1027) I have discussed den raids as a means of rattlesnake control and as a source of live specimens.

## PERSISTENCE OF DENS

That the same sites are used as dens over periods of many years, if the population is not exterminated by man, is evident from the following:

While with relatives in Craig, Colorado, I visited a big rattler den at the so-called Fortification Rocks a few miles north of Craig. The formation is a large igneous dike running east-west. It was too early and cold for the snakes to be out, but the rocks were strewn with vertebrae of the snakes killed in previous years. My uncle and cousin have both gotten great numbers of rattlers at this den. My father told me of killing a great many there when he was a boy. *Robert Finley, Jr., Burlingame, Calif.*



A ranchman recently guided me to a place where there had been a den 25 years ago. After some search the identical spot was located and there was evidence that the den was still in use. Rattlers rarely abandon a place for hibernation as long as it remains a suitable protection. *A. M. Jackley, Pierre, S. Dak.*



In Scott Valley, rattlesnakes are quite numerous and a few dens have been located and are known to many of the local residents. One large den on the east side of the valley has been visited often during the last 25 years, and has been blasted with dynamite; others have gone there with guns seeking sport in killing the snakes. As high as 125 have been reported killed in a day. Yet this particular den is still in use. *Harvey E. Zink, U. S. Forest Service, Sawyers Bar, Calif.*



Rattlers were first found at a certain den near here 25 years ago. Then they were overlooked and forgotten for some time. On the 25th of April this year the same person who found them years before happened upon them, after having forgotten them for so long. Within the next 20 days several parties raided this den, catching a total of 74 rattlers. *Victor E. Jones, University of Idaho, Pocatello, Idaho.*

These seemingly permanent dens are in rock formations. As has been pointed out, prairie-dog holes gradually lose their usefulness as they become filled up by drifting sand or earth, for the new reptilian tenants cannot keep the galleries cleared as did the original excavators. Thus, from time to time, the rattlers must occupy new towns and dispossess the dogs. But in rocky sections the situation is different, and it is evident that the same site, once having been found satisfactory, may be used every winter for many years. Chittenden (1903, vol. 1, p. 47) mentions an instance in which a Capt. LaBarge returned to a den after many years' absence and found the rattlesnakes still using it.

Netting (1932, p. 6) is of the opinion that the same individual rattlers, barring accident, return to the same den year after year, and with this logical opinion several of my correspondents agree. Curran (1935, p. 334) took a contrary view. Woodbury and his associates (1951, pp. 5, 11, tables 1 and 2) in their study of a den of Great Basin rattlesnakes near Salt Lake City over a period of 10 years, proved, by marking specimens, that many returned to the den year after year.

Noble and Clausen (1936) have investigated the senses employed by certain kinds of snakes—not rattlers—in trailing each other to suitable dens. The senses of sight and smell were found of primary importance. It may be presumed that the same senses are used by rattlers. But only some form of homing instinct can explain how the first comers of each season find their way back.

## SPACING OF DENS

The distance between dens, affecting the distance that the average rattlesnake must traverse to reach its winter retreat, is a matter of interest, but dependable data are not at hand. This will no doubt eventually be studied by the marking of snakes, thereby ascertaining their wanderings. Barton (1805, p. 167) mentions rattlers that crossed a river and went as much as a mile to and from a den. Hudson (1903, p. 321; first edition 1892) stated that these snakes travel from 20 to 30 miles to reach their dens; this was repeated by Lydekker (1896, p. 241). Neill (1948, p. 113) thought that canebrake rattlers might converge from 20 miles away to reach an area of limestone caves in the Savannah River swamp. That they travel any such distance as 20 miles is to be seriously doubted. Upon this matter of the spacing of dens, A. M. Jackley commented:

Most rattlers, in years past, wintered in prairie-dog towns, on the prairie and in rolling country, but the various campaigns that have been carried on to rid the country of the dogs makes it uncertain as to the distance between colonies of snakes. Even when the dog towns were numerous and fairly close together, one would find these snakes hibernating in one place but with scarcely any in other towns reasonably close by. It is my belief that dens where large numbers hibernate, say 400 or more, are rarely closer than two miles; and when that close the snakes from such dens intermingle to some extent.

As to the spacing of dens in rocky areas in South Dakota, I believe a brief description of conditions on Table "Mountain" in northwestern Harding County will afford a fairly good example. This so-called "mountain" is not unlike many buttes as to elevation but is larger in area than most, having almost a  $\frac{1}{4}$  mile square flat top. This table is capped with a layer of sandstone about 50 feet thick. Below this cap there are benches and broken rock masses, and the snake dens are on these benches. There has been, and still is, a large concentration of rattlers in these dens, though about 2,000 have been killed during the last three years. I have 10 dens located and they are about 400 yards apart. On one side there is a distance of  $\frac{1}{4}$  of a mile or more with no cavities.

We have a few buttes, some of which are more like ridges rising abruptly from the surrounding prairie, that present extensive rock ledges. Where I find a large colony of rattlers hibernating in such a ledge, I call it one den even though they may group in several cavities that are from two to three hundred feet apart. I don't find any hibernating in loose rock-slides. The reason is in sub-zero weather the circulation of air under a pile of rock renders it unfit.

Southeast of Wood, South Dakota, there is such a rocky butte or ridge. Along the ledge for a distance of about 600 feet, more than 2,000 rattlers were killed. Although large numbers entered five distinct and separate cavities, others merely occupied various random crevices. Just one mile from this place and on a nearby butte, there was another colony of about 500 rattlers. This was to the east; and to the west, a little over a mile, was a smaller group.

There is no question but that in such large concentrations one may expect most any suitable cavity to be occupied. This is similar to the situation in a dog town where several hundred spend the winter. There isn't enough space in any one hole, but even so, they may crowd some holes to an uncomfortable extent, leaving other holes untenanted.

Jackley thought the distance that prairie rattlesnakes traveled away from their dens in the summer was governed by food supply. He thought that most of them had summer ranges within  $\frac{1}{4}$  of a mile of their den, but a few might travel 2 miles or more. Other comments giving suggestions of den separations are as follows:

By what I saw and was told by the ranchers in the vicinity, many rattlesnakes denned near the top of a certain butte at a den located in a crevice in large rocks. During the last of August and September, rattlesnakes were seen migrating toward the den for a radius of

several miles, the snakes being very numerous at the den and in the close vicinity. During warm days in late fall, the snakes were seen near the entrance of the den entangled in large groups. *Vaude L. Wintersteen, Longmont, Colo.*



I know of three *horridus* dens in about one square mile in each of the following Pennsylvania counties: Cameron, Somerset, Warren. There may be a den every mile or so on favorable rock-ledge facings along a main stream. The side hills that form the contributing hollows to a major stream have many rocky points and rock slides, some of which are dens. My guess is one den per square mile in many of the rocky, brushy areas of western Pennsylvania that are known to have rattlers, remembering that what I call a single den may include 2 or 3 concentrations in a single ledge 300 to 1,000 feet long. In areas where exposed shattered rock is not common, there are generally fewer dens and fewer rattlesnakes. *Stephen H. Harwig, Pittsburgh, Pa.*

I judge from the comments of several of my correspondents that in rocky areas, where suitable crevices are likely to be closely spaced, the dens are so selected that the tenants seldom need travel over a mile to reach one. I have elsewhere quoted Paul J. Martin's statement that 7 or 8 dens, yielding 350 to 400 northern Pacific rattlers each season, were found in an area of 10 acres; and there were 15 dens within a radius of 5 to 7 miles. A. C. Mackie has mentioned a mile-long rock face that contained 5 or 6 dens. In these rocky areas, dens are sometimes so close together it is difficult to decide whether they should be considered separate aggregations.

The most important work on the distances that rattlesnakes cover in their summer travels, as determined by the marking of snakes and their later recapture, has been that of Fitch (1949a, p. 539). These researches are mentioned in detail in connection with summer prowling. Unfortunately, for solving the particular problem here discussed, namely the distance that snakes travel to reach winter quarters, the data developed are not especially valuable, since the northern Pacific rattlesnakes in the area under study by Fitch do not congregate for hibernation in large groups, but find refuge, in that mild climate, in makeshift hiding places nearby. We may conclude that, in more severe climates, the distance traveled to a den varies with the intervals between suitable accommodations. The distance traversed is probably rarely over a mile or so at most, for otherwise the fatalities resulting from sudden cold snaps would be excessive. Probably, in areas where dependence must be placed on mammal holes rather than on rock formations, and where colonies of gregarious mammals such as prairie dogs are not available, recourse is had to scattered single holes or sets of galleries. No attention would be attracted to these, as is the case in a den in a prairie-dog town, for the concentration of snakes in the spring or fall would not be great enough to be conspicuous. Undoubtedly, such scattered mammal holes comprise the refuges resorted to by sidewinders and other desert rattlers in the deserts of the Southwest.

#### METHODS OF FINDING DENS

There is a marked difference in most areas between the frequency with which snakes are encountered when dispersed throughout their summer ranges, and their concentrations about the dens during the spring and autumn lying-out periods. In the one case they are scattered, usually in hiding, and largely nocturnal, so one gets the idea that they are relatively scarce; whereas during the latter sea-

sons the impression is given of very large populations. Such of the early travelers in the west who happened upon prairie-dog towns at these seasons reported the congregation of great numbers of rattlers, which others, at other seasons, found difficult to believe. For example, Wheeler (1926, vol. 1, p. 309) tells of the surprise of a party on the upper Missouri in 1872 at the great numbers of rattlers seen at prairie-dog towns and amid rocks. They must have come upon the snakes during the lying-out period, and naturally they were amazed at the large numbers of snakes, compared with the scattered few they may have met elsewhere during the summer.

Most dens have been located by discovery of the rattlers at these lying-out seasons, although experienced hunters such as A. M. Jackley have been able to recognize them, even while untenanted in the summer, by various signs of occupancy. Others are found by observation of the directions taken by the snakes during their annual pilgrimage toward the dens, the population density increasing as the focal point is approached. At such times great numbers of snakes are killed, either intentionally or otherwise, if their routes happen to cross a major highway.

A rattlesnake den may be found if one will notice which way they travel late in September or early in October. I have watched many a snake and followed it up and found small dens of 16 to 25 in woodchuck (or ground-hog) holes, but the larger dens I have found in rock ledges. *Gustave W. Koski, U. S. Fish and Wildlife Service, Windham, Mont.*



In Utah, the rattler habitat for the most part is the scrub oak-sage type, mostly rocky slopes, where lizards abound; in Idaho, the sage types in ledgy slopes and rocky flats. In the upper Snake River basin, great areas of lava beds abound with them, and often large dens are found there in the fall. I have seen only a few in such gatherings, but a number of my stockmen friends have told of coming upon great numbers in the vicinity of lava-bed caves. A particular gravel road along the foot of several lava-bed hills seems to be preferred at certain seasons of the year. On some strips I have noted scores of them lying in the road, all heading in the same direction, usually down country in the spring, and upward toward fall. *C. H. McDonald, U. S. Forest Service, Stevensville, Mont.*



While in Colorado I was fortunate in witnessing a seasonal migration of rattlesnakes in the San Luis Valley, between Mineral Hot Springs and Saguache. Here the rattlers den up in well-weathered volcanic rock for the winter. Then, after the frost has gone, they migrate out into the valley by the hundreds for the summer, to feed on small rodents. In the fall they return to the rocks. During the migration hundreds of these snakes cross the highway, and many are killed by being run over by passing cars. *Carl Hammarstrom, U. S. Forest Service, Rochford, S. Dak.*

A typical newspaper report of a similar situation is the following, from the *Denver Rocky Mountain News*, October 24, 1937:

The State Highway Courtesy Patrol reports thousands of rattlesnakes are migrating northward in Weld and Morgan counties and that automobiles have killed at least 1,500 between Wiggins and Roggen [18 miles] on U. S. Highway 81. The venomous snakes range in length from one foot to two and a half feet, highway patrolmen reported. The number killed represents only a small portion of the vast movement of the snakes at what is called "denning time."

Victor (1870, p. 214) has told a story of how Meek, a well-known trapper of pioneer days, once took refuge from a violent thunderstorm under a shelf of cliff.

Rattlesnakes started to go by, first in small groups, and finally in hundreds and thousands, on their way to a den. The ground was alive with them, and he and his horse were cornered until the swarm had passed.

Neill (1948, p. 113) believes that rattlesnakes have courses to their dens that they persist in following, despite changes in surroundings. One such trail was through a pine forest that the canebrake rattlers used even after the forest was cut down; another was through a suburban section of Augusta, Georgia. Woodbury (1951, p. 4), who located many large dens of *C. v. viridis*, *C. v. decolor*, and *C. v. lutosus* in western Colorado and in Utah, did so by watching the snakes approach or leave the dens, or by finding cast skins, particularly racer skins, at the entrances.

#### LIFE AT THE DENS

Since a rattlesnake den is a place of refuge and concealment, little is known of the life of the snakes during actual hibernation. Road and mine excavations that have opened dens in winter have supplied some observations. Safe in their retreat below the frost line, they are found to lie torpid and virtually motionless, in groups of masses—"balls" as they are often termed—until aroused by the spring warmth.

Upon their habits on the surface during the lying-out period, more complete field notes are available. For, at midday, when the weather is favorable, they gather about the dens, separately or intertwined in groups, to take advantage of the last warmth of the autumn, or the first reviving sun of spring. Usually they lie close to the holes so that they may quickly find sanctuary if danger threatens. Coming unexpectedly upon one of these concentrations of rattlesnakes is sufficient to startle even the hardest hunter or fisherman. They are particularly striking sights at prairie-dog towns, where the topography is such that more can be seen from a single vantage point than is possible amid tumbled rocks and boulders.

The exact time of year when these lying-out concentrations may be found depends on latitude, altitude, exposure, and year-to-year temperature variations. The following observations give some data on seasons and hours, and the actions of the snakes when discovered:

The northern Pacific rattlesnakes, here in the Northwest, start heading back to their dens in late August and September, and some climb 200 to 500 feet, and even 1,000 feet from a creek up the steep cliffs, winding their way to the den, which is hard to get at sometimes, and in a dangerous place.

They start coming out of the den about the 20th to the 25th of March in an early spring. They don't leave the den at that time, but just make an appearance at the surface to warm up in the sunshine. They come out about 10:30 or 11 o'clock, and re-enter between 3 and 4 in the afternoon. They do this coming out and going back every warm day for nearly three weeks before they start spreading out in every direction from their dens, staying out a little later each day in April, until finally you can't find one around the den much after the first of May. Sometimes you will see 100 rattlers sunning themselves at a den about the 10th of April. *Marion E. Rose, Pateros, Wash.*



Success in catching or killing rattlers depends on ample leisure and immunity from fatigue during the early spring when they are at or near their dens. This period may last only a fortnight, if temperatures by day and night are consistently high, or it may last a month, or even six weeks, if the night temperature remains low. Hay must be made while the

sun shines. The fall campaign from early September to mid-October is less productive of results, as the snakes either retire into their dens for good as soon as they arrive there, or lie in the very mouth and disappear at the tremor of one's footfall. In spring, the normal program is as follows: For the first week or more they leave the den as soon as the sun is high enough to strike the site, and lie coiled up, sometimes in a solid mass, on the flat, naked rocks at the mouth, retiring again toward the end of the afternoon. If no rockslide is handy, this period may be much extended; if, however, a rockslide is contiguous, the larger ones at first, and the smaller a little later, will descend to it, lying wholly or partially exposed during the day and seeking refuge at night in the lower strata of the slide. The larger specimens, especially the females,<sup>5</sup> soon leave this retreat and go in search of a marmot hole in which they make their headquarters till the young of these animals provide them with their first substantial meal of the season. When the young marmots are too big to be swallowed, the rattlers leave the steep hill-slopes and come to the bottom-lands for the summer. They choose as their headquarters either a patch of thick brush or an isolated boulder, in or under which they doze away the day in shelter and security. As soon as the rocks in a slide become uncomfortably hot, all the snakes therein trek to lower levels. If a den is on the chine of a hill, some snakes will spend the summer on the plateau behind it while others will seek the valley bottom. *A. C. Mackie, Vernon, B. C.*

C. B. Perkins, in his raids on prairie rattlesnakes in dog towns near Platteville, Colorado, had his best success in the fall, although his operations, covering only two campaigns in each season, were hardly extensive enough to prove which season is the better. There is no doubt some variability from year to year, depending on temperature conditions during the lying-out days at the dens. The statistics of his catches, which totaled 863 rattlesnakes, are set forth in table 8:5.

Concerning his experiences at the dens, Mr. Perkins wrote:

At these dog towns it was noticeable that we would see no rattlesnakes at all at first, and then, a few minutes later, the same place would be full of them. Usually the first couple of snakes would be large ones and would be going somewhere—not right close to holes. Twice I was startled by the rattling of a snake I hadn't seen first, and although both times I almost stepped on the snake, it didn't strike.

As I've always found to be the case, all the snakes try to get away by scrambling down the nearest hole; and, when cornered, the smaller the snake (except the button babies), the more they fight and the harder they are to catch. The prairie rattlesnake, by-the-way, resents being caught more than any other rattler I know.

The air temperature range for the three days of our largest catches in 1930 was:

Oct. 12—63° to 36° F.

13—63° to 34° F.

14—66° to 35° F.<sup>6</sup>

The warmest part of the day was from noon until 2 P.M., but the hunting was better from about 10:30 to 1:00. Also, we became very tired about one o'clock, and possibly were not working so hard or covering so much ground as before. The nights were really cold, but it seemed to make no difference to the snakes whether the holes sloped south and got the sun, or sloped north and still felt cold to the hand at noon.

It will be observed from Mr. Perkins' records that the peak of the lying-out season in the spring, at the latitude of Platteville, Colorado, is about April 18, and of the autumn October 13. Of particular interest is the length of the lying-out period, which makes a den a fruitful place for collecting, whether in the fall or spring, although the former appears somewhat better.

<sup>5</sup> Other observers have found that the males are the first to leave the dens in the spring, and the first to arrive in the fall.

<sup>6</sup> Dyche (1909, p. 312) also observed that snakes came out of the dens to sun themselves on good days, even after it had become quite cold at night.

TABLE 8:5  
DAILY CATCHES OF PRAIRIE RATTLESNAKES MADE BY C. B. PERKINS  
AT PRAIRIE-DOG TOWNS NEAR PLATTEVILLE, COLORADO

Spring 1930		Spring 1931		Spring 1932	
		Date	Catch	Date	Catch
No hunts made		April 12.....	12	April 3.....	1
		15.....	10	12.....	20
		16.....	9	14.....	18
		19.....	17	17.....	56
				18.....	36
				20.....	31
				May 1.....	35
				2.....	17
				5.....	3
Total.....			48		217
Fall 1930		Fall 1931		Fall 1932	
Date	Catch	Date	Catch	No hunts made	
Oct. 12.....	17	Sept. 30.....	24		
13.....	93	Oct. 3.....	6		
14.....	64	4.....	25		
Nov. 3.....	16	6.....	12		
		9.....	34		
		13.....	90		
		14.....	99		
		17.....	31		
		18.....	79		
		21.....	8		
Total.....	190		408		

A. M. Jackley agreed with Mr. Perkins that fall collecting is more fruitful, rather than spring, as found by Mr. Mackie. Mr. Jackley wrote:

Rattlers leave their dens in the spring gradually, and for this reason many more can be killed in the fall than in the spring. However, if one were to visit a den daily in spring, he could kill a higher percentage at that one den than by visiting the den in the fall. One might kill a hundred or more at a den in one day in the fall, but 25 would be a large number in the same length of time in spring. The period of emergence in South Dakota normally extends from about April 25th to May 15th. They begin returning to the dens in the latter part of September and continue through most of October.

With reference to seasonal variations in denning dates, owing to year-to-year fluctuations in temperature, Mr. Jackley continued:

The fact that some rattlers emerge from hibernation earlier than previously recorded led me to believe they would abandon their dens earlier than usual in a warm spring, but at this time the evidence indicates they will not. The few that came out in late March and early April this year, save an occasional exception, returned into the dens. Two rattlers entered one trap<sup>7</sup> on March 26th, and during the first two weeks in April the largest number

<sup>7</sup> Jackley placed traps at the den exits so that the rattlers were caught even if they were only leaving for a midday sun bath.

caught was 8. Others began entering traps around April 25th. It was not until May 5th and 6th that considerable numbers began to show up. So the conclusion is that notwithstanding we had unusually warm weather, 90 to 95 per cent of these snakes were content to remain in their dens almost until their usual time for scattering. Although their migration from the dens may be under way a week earlier than in other years, this movement will not take place as soon as anticipated.

Also, these snakes came out of their dens in Harding County in northwestern South Dakota at approximately the same time they did down near the Nebraska line. This is one thing I have long wanted to learn and which could scarcely have been accurately determined except by use of the traps. Local weather conditions naturally have made this study difficult, but it now is quite evident that with rather uniform weather conditions they will emerge in the spring at the same time throughout the western half of South Dakota.

Although Mr. Jackley's observations tend to minimize the effects of year-to-year temperature differences, no doubt there is some seasonal variation, similar to that reported by Volsøe (1944, p. 12) in the case of European vipers, so closely do snakes react to temperatures. In a cold spring their exit and spreading into their summer ranges may be delayed by two to three weeks or more. In the fall a gradual drop in temperature turns them toward their dens; and, should there be a sudden unseasonable freeze, they may be caught too far from their dens and must seek makeshift retreats or die. So closely dependent is muscular activity on ground and air temperatures that they may be fatally immobilized only a few feet from safety.

Although Mr. Jackley observed no difference in returning or emerging dates between the northern and southern boundaries of South Dakota, a greater latitudinal range would unquestionably have demonstrated the effects of critical temperatures. The prairie rattlesnakes of the Texas Panhandle certainly have a longer active season than those of South Dakota. In San Diego County an altitudinal difference is manifest, for the snakes of the mountains come out later than those of the coastal area, with its milder climate.

The following are some additional observations made by my correspondents on rattlesnake habits during the lying-out periods:

The rattlesnake dens are in caves or crevices of the rocks; sometimes several hundred are in one den. In February or March, when the warm sun comes out after a shower, they will crawl out and lie in the sunshine. We have had snake drives in the Wichita Mountains and killed as many as 150 in or near one den. Sometimes ten or fifteen will roll themselves together; and, in at least one instance I know of, twelve were killed at one shot from a shotgun. *L. E. Crawford, Supt. State Game Ranges, Lawton, Okla.*



Four or five years ago I came over to this locality to hunt coyotes in the middle of April. I was on horseback, and about two miles from camp I killed a rattler that was trying to cross a snowbank. Riding down the draw about two hundred yards, another big rattler struck at my horse. He was lying in some rocks in the sun. Killing him, I rode on down the draw about 100 yards more and saw three more rattlers on one rock. I turned and rode up around the rocks so as to get above them. Then I had snakes all around me. Three or four of them started to rattle and my horse got nervous. I then realized I was on the edge of a snake den. Before I got clear of the rocks there must have been 25 or 30 snakes all rattling at the same time, and these were only a few of the ones in sight. That den had more snakes than any other den that I know of. It was a big adobe bank about 35 to 40 feet high with crumbled rocks on top and at the bottom. That day the sun was shining warm and they had come out in spite of the snow. I don't know how many snakes there

were but the whole side of the slope was covered with them. A sheep outfit dynamited a den of rattlers about six miles from this place and killed around 600 rattlers. *Eddie Buchta, Fish and Wildlife Service, Moneta, Wyo.*



At the dens I have seen rattlers in groups of from six to several hundreds. They coil themselves around one another until they make a sort of ball. I can't say how long they stay this way, but I know they stay twisted up in this way for as long as two days, and I have seen bull snakes twisted in the same balls with the rattlers. I have seen from 20 to several hundred rattlers using a den. All the dens I have found have been in rock cliffs, or sand and clay banks. *Ellen Johnston, U. S. Fish and Wildlife Service, Shelby, Mont.*



I ran into a den in May near Spion Kop, Montana, on the side of a hill having a big rock ledge some quarter of a mile long. There was a huge pile of rattlesnakes in front of a crack in the ledge. I was hunting coyote pups at the time and it took me by surprise to see this pile of snakes there in the sun on the south side of the hill. Having my .22 rifle with me, I started to shoot into the mass, killing and crippling 19 rattlesnakes, averaging 30 to 33 inches in length, together with a few little ones. *Gustave W. Koski, U. S. Fish and Wildlife Service, Windham, Mont.*

Other data on rattlesnakes lying about their dens in the spring and fall will be found in chapter 14 on control (p. 1027); and climatic and temperature effects are further treated under temporal activity in chapter 7 (p. 430). Several of my correspondents have commented on the wariness of the rattlers during the lying-out period (see also Gloyd, 1946, p. 92). At the first disturbance or threat of danger they take refuge in the holes or crevices. The slightest movement of an intruder causes one or more to rattle and the alarm spreads contagiously. A. M. Jackley wondered how they all became so quickly aware of danger if they are indeed deaf; many observers have naturally assumed that the rattles sound the alarm. As discussed in chapter 6 under senses (pp. 392, 406), it is probable that their sensitivity to earth-borne tremors suffices to transmit the alarm to those that have not actually seen the intruder. This is a kind of hearing, although not through air-borne vibrations, as the term is usually understood. Gillam (1916, p. 132) heard a number of snakes rattle at a den when one was being caught. An individual 80 yards away seemed to sense the disturbance and rattled.

Stephen H. Harwig of Pittsburgh had this to say about the actions of *horridus* in western Pennsylvania when disturbed during the lying-out period:

When annoyed at a den, the rattlers tend to take refuge under rock slabs, rather than in the deep vertical fissures, of which there are many in the face of a ledge. Rattlers are very fond of lying in brushy fissures 6 to 30 inches wide and 4 to 20 inches deep, between rock slabs. When disturbed they quickly glide under one of the rocks. Only rarely will they hurl themselves into a hole or crevice more than 2 or 3 feet deep. Occasionally, when partially blinded by incipient shedding, they will crawl hastily and erratically over crevices and sheltering slabs in an effort to escape.

In their descriptions of rattlesnake dens, observers frequently refer to balls of rattlesnakes, sometimes disclosed by winter blasting operations when a den is opened to sight, and at others by people who have observed them on the surface during the lying-out periods. E. R. Hall (1929, p. 80) was told of balls of Great Basin rattlers that were found in the fall lying-out period at a den in eastern Nevada. Ala Jones (1947, p. 48) saw masses of rattlers as large as wash tubs. Rollinson (1944, p. 187) saw a ball of prairie rattlers as large as a watermelon.

Dobie (1946a, p. 12) repeats the Rollinson account and adds two others from Mexico. Morgan (1939, p. 363) says the balls may contain from 2 or 3 to hundreds of snakes. It has been suggested that these masses of rattlesnakes are composed of snakes indiscriminately mating or endeavoring to mate, but there is nothing to substantiate such a presumption. Balls of rattlesnakes within a den, by reducing the surface-mass ratio, would minimize heat and moisture losses and would save space as well. There is thus no reason to question such observations as the following:

Workers in limestone quarries have noted large balls of hibernating rattlers of all sizes exposed by blasting operations in the winter months. These balls are often one foot in diameter. *V. A. Shaffer, State Conservation Officer, Murray, Iowa.*



In the adjoining foothills there is a range of sandstone and limestone hills in which the rattlesnakes are very numerous, and there they seem to den up in the holes and small caves in this soft rock formation. A farmer told me that he and his hired man found in one of those caves a ball of rattlesnakes which contained more than 100 snakes. *Ray M. Bradshaw, U. S. Forest Service, Woodland Park, Colo.*



I have seen dens of snakes blasted out—big balls of them—around Plains and Paradise, Montana, years ago. *P. Bruce Centerwall, U. S. Forest Service, Tonto Basin, Ariz.*

However, there is less likelihood that the balls of snakes seen outside the dens during the lying-out period represent accurate observations. Presumably there is here some exaggeration, such as might be induced by the exciting circumstance of coming upon a pile rather than a ball of rattlers at the entrance to a den. For, under such conditions, balling up would defeat in some degree the primary reason for lying out, namely to be warmed by the sun. But that the snakes sometimes pile up in veritable masses at the entrance to a den there can be little doubt.

#### ONTOGENIC DIFFERENCES IN DENNING

The opinion has been expressed by A. M. Jackley that the young-of-the-year do not den with the adults and adolescents in rock-crevice dens, although they may in prairie-dog-town dens, as was verified by the composition of catches made by C. B. Perkins. Mr. Jackley wrote:

One of the most surprising things to me is the fact that only in a few instances have I found young rattlers in the spring at the dens. These few exceptions have been in dog towns where a large colony hibernates. Large dens in buttes, cracked open banks, and sink holes rarely have any really young ones in them. In many dens in buttes where several hundred have been killed, not more than 2 or 3 per cent were young born that year.

My traps accurately check the snake population in a den. The juveniles have no difficulty entering a trap, and what few there are, do so. I am convinced that young born only a quarter of a mile away from a den, will not follow the older ones to the den the first fall. I have found young in burrows dug by striped gophers [ground squirrels] and pocket gophers. I think they spend their first winter in mammal holes such as these. It is different where the den is in a dog town. Probably the young were born in some hole in the town, or not far away, and when winter comes there are plenty of holes in which to be safe.

It may be suggested that the greater dispersion of hiding places in a dog town may protect the young from being crushed, as they would be in the crowded spaces of a fissure den.

These inferences, regarding the separate denning of the young-of-the-year

among the prairie rattlesnakes (*C. v. viridis*), have been verified among the Great Basin rattlesnakes (*C. v. lutosus*) by Woodbury and Hansen (1950, p. 67) and among the timber rattlesnakes (*C. h. horridus*) by Swanson (1952, p. 180). One of my correspondents expressed the opinion that mother northern Pacific rattlesnakes (*C. v. oreganus*) returned to the vicinity of their dens before giving birth to young, so that their broods might have no difficulty in locating the ancestral refuge. This is contrary to the opinions previously quoted.

Messeling (1953, p. 21) has evolved a number of highly doubtful theories as to how a mother rattlesnake conducts her young to their first hibernations. Speaking of *horridus* in Wisconsin, he expresses the opinion that a mother rattlesnake first leaves her young in order to feed up for the winter. She then returns to them and leads them to the den, rattling as she goes. If she fails to return for them, they are unable to find their way to the den, and most of them will be frozen. When young snakes are taken to a den by the mother, they remain in the den during their first year, feeding on insects.

#### ANIMALS THAT HIBERNATE WITH RATTLESNAKES

*Prairie Dogs and Owls.*—That other animals hibernate with rattlesnakes is well known, several kinds of harmless snakes being the most frequent cohabitants. Before discussing these, it may be well to dispose of the ancient myth of that happy family of congenial lodgers, the prairie dogs, burrowing owls, and prairie rattlesnakes. The story started, of course, from the sight of prairie dogs, owls, and snakes scattered at the mouths of the prairie-dog holes, from which observation it was supposed that they were peaceful tenants of the same holes. This was more a bit of folklore than a myth, propagated—as have been some of the rattlesnake yarns—by the early-day natural histories, for its truth was denied at a relatively early date by some of the western travelers.

The owl-dog-rattler association was observed by such early explorers as Lewis and Clark in 1804–6 (Coues, 1893, vol. 1, p. 166) and by Pike in 1805–7 (Coues, 1895, vol. 2, p. 431). Latrobe (1836, vol. 1, p. 237) reported that burrowing owls, rattlesnakes, and badgers were found with prairie dogs. Murray (1839, vol. 1, p. 207) repeated the story, but said he saw no rattlers in the prairie-dog towns. Wied-Neuwied (1843, p. 141) thought the rattlers used only abandoned prairie-dog holes. Gregg (1844, vol. 2, p. 230) thought the owls and rattlers to be intruders that lived on young prairie dogs. G. W. Kendall (1844, vol. 1, p. 189—see also Marcy, 1850, p. 185, and Audubon and Bachman, 1854, vol. 2, p. 326) reported that a rattler had eaten a young prairie dog and that the snakes were loafers appropriating the dogs' holes. A similar view was expressed by Bartlett (1854, vol. 2, p. 561) and by Parkman (1872, p. 361). Cremony (1868, p. 292) reports the Apache Indians as saying the rattlers are wise enough to let the prairie dogs build their homes for them. Other early denials of the symbiotic story are given by W. A. Bell (1869, vol. 1, p. 32), Victor (1870, p. 216), Sternberg (1869, p. 156), Coues (1874, p. 324), Williston (1878, p. 203), Brons (1882, p. 565), and Majors (1893, p. 105). Coues gives a particularly effective summary of the relationship:

As to the reptiles, it may be observed that they are like other rattlesnakes, dangerous, venomous creatures; they have no business in the burrows, and are after no good when

they do enter. They wriggle into the holes, partly because there is no other place for them to crawl into on the bare, flat plain, and partly in search of owls' eggs, owlets, and puppies, to eat.

I have the following note in the handwriting of Frank Stephens, a naturalist who lived for many years in San Diego, and after whom the rattlesnake subspecies *stephensi* was named:

In western Kansas in September, 1874, I noticed a prairie dog acting in an unusual manner. It would run toward the entrance of its hole and then back away, then start for the hole from another direction. It did this several times, and at last made a quick dive down the hole from the other side. I walked over to the hole and near the edge lay a rattlesnake curled up. It was conclusive evidence to me that the prairie dog knew the danger of the snake, kept out of its way, and that the dog and snake would not live in the same home in harmony as has so often been written.

Ringle (1924, p. 19) reported that a prairie dog would not enter a hole containing a rattler. He put carbon disulphide on a dog, upon which it started down one hole and then returned. It then went down another hole and stayed. He put the volatile, ill-smelling fluid on a corncob and shoved it into the first hole, whereupon a rattler came out. Dixon (1928, p. 296) dug out at least 25 ground owls' nests and found neither rattlers nor squirrels in any of them. Seton (1929b, p. 294) well summarizes the prairie dog-owl-rattler happy family as a "venerable joke." King (1955, p. 33) has contributed new observations on the prairie-dog-rattlesnake relationship.

Upon this subject my own correspondents have made the following interesting observations:

I have seen rattlesnakes take possession of a prairie-dog town in the fall; all the dogs, owls, and rabbits moved out when the snakes moved in. This place was on the Sand Arroyo Creek in Morgan County, Colorado. There were some 2,000 rattlers killed there in the fall of 1939. That is the largest congregation of snakes I have ever seen. *Charles G. Holzworth, Kremmling, Colo.*



Recently I parked my car centrally in a small prairie-dog town where the snakes were dispossessing them. The dogs wouldn't enter their holes, that is, most of them wouldn't. I could see several snakes at a time, apparently exploring the various holes to determine which suited them best. After watching them for more than an hour, I slowly and quietly walked around and found that the dogs were so confused that I could walk right up to them. *A. M. Jackley, Pierre, S. Dak.*

Thus he believed that when snakes and dogs are found together, it is during the transition period when the rattlers are taking over a town. In 1931, C. B. Perkins had this to say about the Platteville towns from which he took more than 800 rattlers during a period of three years:

A thing that intrigues me is the fact that we got snakes on the edge of holes that had fresh prairie-dog droppings, and also from the 3 or 4 holes which were inhabited by burrowing owls. When we stopped the car we could see and hear the dogs, but saw nothing more of them while hunting. The owls, however, we occasionally saw. So there must be considerable confusion as the snakes move in.

MacClary (1939b, p. 30) reported that a man turned several rattlers loose in a prairie-dog town, and that the dogs were driven out within 3 years. Osborn and Allan (1949, p. 322) reported on a populous prairie-dog town that was being

protected as a subject of ecological study. The population gradually declined and eventually disappeared, and although the authors attribute this to changes in vegetation, rattlesnakes were found in the town, and the refuge manager thought they might have been in part responsible for the prairie-dog decline.

McDaniel and Taylor (1877, p. 272) made the ingenious, but highly improbable, suggestion that the prairie dogs preferred to live in the company of rattlesnakes because of the protection from wolves and other enemies that the snakes afforded them. Walker (1952, p. 81) thought the happy-family myth may have gained credence because the young owls are able to mimic closely the sound of a rattlesnake's rattle. F. Simpson (1915, p. 279) claims that rattlers are afraid of being interred by prairie dogs, and that if one starts to fill the entrance to a burrow, any snake within will come out at once.

The rattlers do not return for very many winters to the burrows from which they have dispossessed the dogs, since, without the care of the latter or other mammals, the holes soon fall into ruin. Hence there is a continual process involving the construction of new towns by the dogs and eventual eviction by the snakes. But no doubt the dogs so outnumber the snakes that many are undisturbed for years.

That the joint-lodging story still persists is indicated by the following report lately received from one of my correspondents: "Rattlesnakes are found in prairie-dog towns, as prairie dogs, owls, and rattlesnakes live in the same burrow."

*Other Snakes.*—So inherently vicious are rattlesnakes popularly—but erroneously—supposed to be, that visitors at the Zoo are frequently heard to express surprise that more than one can be kept in a cage without a fight ensuing. But as these notes amply show, not only are they peacefully gregarious, but other genera of snakes may join them in their winter seclusion. At the San Diego Zoo we keep a mixed cage of rattlers and bull snakes to illustrate this amicable association.

The real codenizens of the dens with rattlesnakes are other kinds of snakes. Their presence is quite frequent, even usual, as the following observations indicate:

The men who tended the rattlesnake traps which I had set at dens kept count of rattlers only, and they totaled 133. They told me about a dozen bull snakes and possibly 40 blue racers were also caught. The fact is, I have never found a den in South Dakota that did not contain bull snakes and blue racers; and when the den is reasonably close to water, there are usually garter snakes as well. However, I have not found bull snakes congregated in large numbers in any one place. From my experiences with traps at dens, I believe that the blue racers, bull snakes, and garter snakes leave earlier than the rattlers in the spring.  
*A. M. Jackley, Pierre, S. Dak.*



In May of 1944, about the 5th, I set a trap at a den of rattlers. This trap was of a type devised by A. M. Jackley. About the 10th, there were 5 rattlers and one blue racer in the trap. They continued to get into the trap until about the 8th of June. On the 20th, I took up the trap and had a total of 25 rattlers and 5 blue racers in it. *Glenn Flathers, U. S. Forest Service, Camp Crook, S. Dak.*



One of the most unusual circumstances to come to my attention happened last year. Don Kortés, of Leo, Wyoming, found a den of snakes and dug a pit in which they were trapped when they came out in the spring. The surprising thing to me was that the rattlesnakes had hibernated in the same den with bull snakes, blue racers, and garter snakes. A total

of about 350 snakes were taken and about an equal number of each of these species was found. This would tend to contradict the old theory of the enmity between rattlesnakes and bull snakes. *Don S. Simpson, Deputy Game Warden, Saratoga, Wyo.*



I know there is a general belief that bull snakes will kill rattlesnakes, but I have seen them denned up in the same den. I once killed 200 rattlesnakes at a den and there were about 20 bull snakes in the same den. *Ernest Gutzman, U. S. Forest Service, Winsper, Idaho.*



It is commonly thought that the nonpoisonous bull snake kills and eats rattlers, and for this supposed virtue, enjoys almost complete immunity from man; but the two species hibernate together and I have taken both in a trap, living apparently amicably together. I have found a rattler, a bull snake, and 5 blue racers all fraternizing together in the trap; the common garter snake also dens up with the rattler. *A. C. Mackie, Vernon, B. C.*



While helping to build a dam in western South Dakota, we dug into a den of snakes in January of 1936. They were coiled up in a round ball 37 feet down in a shale hillside. Sixty-three rattlers and over 100 blue racers and bull snakes were all coiled up together. They did not seem to be alive, but we took some over by the fire and they soon came to life. *Lawrence Kelly, Harper, Oreg.*



The malpais rock, with its many cracks, seems to be a favorite place of hibernation for rattlers. Also, the big rockslides are selected by some of them. Last fall, in one particular malpais outcrop, I found several rattlers, a striped racer, several Arizona ring-necks, and a brown garter, all of which seemed to have chosen this site for their winter home. It was located a short distance from the banks of White River. *A. W. Mollison, U. S. Indian Service, McNary, Ariz.*



We have only the timber rattler here in Pennsylvania. A lot of people are under the impression that the black snake will kill the rattler, but I have found them denned up together several times. *T. J. Cox, State Fish Warden, Coudersport, Pa.*



In Pennsylvania, I have found numerous copperheads and some pilot black snakes living in harmony with timber rattlers at a common den rock during the summer, so all these snakes probably den together to some extent in the winter. Milk snakes, black racers, and garter snakes are sometimes seen in a rattler-den area. I have never witnessed any hostility between snakes at a den. *Stephen H. Harwig, Pittsburgh, Pa.*



Rattlesnakes and copperheads, which are about as numerous as rattlers, den up together; and I have seen them coiled together during cold weather. *B. A. Eger, U. S. Forest Service, Buena Vista, Va.*

Beauvois (1799, p. 375) mentions finding black snakes<sup>\*</sup> and garter snakes in dens with timber rattlers. Ferrall (1832, p. 301) quotes a newspaper report of a den containing 193 adult timber rattlers, 16 black snakes, and a copperhead. Martin (1859, p. 110) reported a den with rattlesnakes, king snakes, and black snakes. Catlin (1868, p. 23) also records black snakes with timber rattlers. J. D. Mitchell (1903, p. 39) located a coachwhip in a rattler den. Erwin (1925, p. 7) found a spotted night snake in a den of Great Basin rattlers. Noble and Clausen (1936, p. 314) excavated a den that was found to contain timber rattlers and copperheads, with black racers nearby. Messeling (1953, p. 23), in Wisconsin, found that the timber rattler associated at the dens with bull snakes, blue racers, black snakes, and blow snakes.

<sup>\*</sup> One cannot be certain, from these reports, whether the "black snakes" mentioned were black racers (*Coluber constrictor constrictor*) or pilot black snakes (*Elaphe obsoleta obsoleta*).

Anderson (1947, p. 2), in South Dakota, found bull snakes, blue racers, hog-nosed snakes, and a milk snake sunning themselves together at a den. Woodbury and his associates (Woodbury and Hansen, 1950, p. 127; Woodbury and Smart, 1950, p. 45; Woodbury, 1950, p. 5) recorded the following codenizens with rattlesnakes, as discovered by capture of the snakes leaving a den: desert striped racer, western yellow-bellied racer, desert gopher snake, desert spotted night snake, regal ring-necked snake, western long-nosed snake, western milk snake, and wandering garter snake. There were about  $\frac{3}{4}$  as many striped racers as rattlers; the western yellow-bellied racers numbered about  $\frac{1}{4}$  as many as the rattlers, and the gopher snakes about  $\frac{1}{25}$ . Of the other kinds of snakes, there were only one or two present in large dens. Swanson (1952, p. 177) found timber rattlers and copperheads in the same den.

Summarizing the data on snakes occupying the same dens with rattlesnakes, we find the following species of rattlesnakes involved:

- Prairie rattlesnake (*C. v. viridis*)
- Great Basin rattlesnake (*C. v. lutosus*)
- Northern Pacific rattlesnake (*C. v. oreganus*)
- Western diamond rattlesnake (*C. atrox*)
- Timber rattlesnake (*C. h. horridus*)

The following species of snakes have been reported denning with them, in instances where the identifications were trustworthy:

- Bull snake (*Pituophis catenifer sayi*)
- Desert gopher snake (*P. c. deserticola*)
- Sonoran gopher snake (*P. c. affinis*)
- Pacific gopher snake (*P. c. catenifer*)
- Pilot black snake (*Elaphe obsoleta obsoleta*)
- Red milk snake (*Lampropeltis doliaata syspila*)
- Western milk snake (*L. d. gentilis*)
- Western long-nosed snake (*Rhinocheilus lecontei lecontei*)
- Black racer (*Coluber constrictor constrictor*)
- Blue racer (*C. c. flaviventris*)
- Western yellow-bellied racer (*C. c. mormon*)
- Desert striped racer (*Masticophis taeniatus taeniatus*)
- Western coachwhip (*Masticophis flagellum flavigularis*)
- Great Plains garter snake (*Thamnophis radix*)
- Eastern garter snake (*Thamnophis sirtalis sirtalis*)
- Washington garter snake (*T. s. tetrataenia*)
- Wandering garter snake (*Thamnophis elegans vagrans*)
- Western hog-nosed snake (*Heterodon nasicus nasicus*)
- Regal ring-necked snake (*Diadophis regalis regalis*)
- Desert spotted night snake (*Hypsiglena torquata deserticola*)
- Copperhead (*Agkistrodon contortrix*)

The benefits of heat and moisture conservation that rattlesnakes secure by aggregation would likewise accrue to any other snakes that den with them, which sufficiently explains their presence. There is little or no enmity between them, although one or two of the species might rarely eat a small rattler during the active season.

*Other Animals.*—It is probable that the associations with other animals that have occasionally been reported are more fortuitous. It is to be doubted whether these go beyond the other animals' accidentally selecting an adjacent refuge.

In one rattlesnake den we found 13 rattlesnakes, 4 turtles, 2 skunks, and a swarm of bees with a lot of honey. We had trouble getting the snakes out because of the bees and had to abandon this den. We have also found mice, mouse snakes, and coachwhips in the dens with rattlesnakes. *John R. Wood, Brownwood, Tex.*



I have known of a road crew bulldozing out dirt in a roadway to expose a den of snakes, all more or less dormant from the cold. In with them were several live but dormant ground squirrels unharmed but waiting for spring. *T. F. Pearson, U. S. Forest Service, Salmon, Idaho.*



I have found skunks and snakes denning in the same den at the same time. *J. D. Bankston, Mason, Tex.*

J. D. Mitchell (1903, p. 39) claims to have found tortoises, rabbits, and skunks hibernating with rattlers. Motl (1936, p. 3) saw a squirrel jump out of a den from which he was extricating rattlers. Messeling (1953, p. 21) says that raccoons and skunks den with timber rattlers in Wisconsin. As long ago as 1774, Goldsmith (vol. 4, p. 131) said that rattlesnakes and armadillos den together; this has lately been reiterated by Beaty (1941, p. 50). Woodbury and Hardy (1948, pp. 172, 192) found that the Great Basin rattlesnake (*C. v. lutosus*) and the Mojave Desert sidewinder (*C. c. cerastes*) sometimes use the dens of the desert tortoise (*Gopherus agassizi*) as winter refuges.

## AGGREGATION AND DISPERSAL

### THE DENNING STIMULI

The denning urge in rattlesnakes seems to be entirely predicated on temperature, a fall of temperature in the autumn starting them toward the dens, as discussed in chapter 7 (p. 430). Southern species often do not hibernate, as noted by Kauffeld (1939, p. 32) in Florida. Our own observations in southern California indicate that snakes may come out at any time during the winter if the weather is favorable. None of the northern species, such as the timber, prairie, and Great Basin rattlers, which hibernate in their native haunts, shows any signs of winter lethargy under the artificial temperature conditions of the San Diego Zoo. Haupt (1915, p. 18) calls attention to the difference between snakes and a mud turtle in this regard; snakes when kept warm did not hibernate but the turtle did. C. B. Perkins tells me that this experience has not been verified at the San Diego Zoo, where the turtles, under our mild climatic conditions, show no tendency to hibernate in winter.

We have no knowledge of what stimuli lead rattlesnakes to the same refuge year after year. Woodbury (1951, p. 11) showed that the same rattlesnakes did return to the same den each winter. Bradford (1946, p. 21) says that the return of snakes to the same den is an indication of territoriality, a sort of property right.

## ADVANTAGES OF AGGREGATION

The question naturally arises as to what advantages rattlesnakes gain by this gregariousness at the time of hibernation. Several possible benefits may be mentioned. One advantage is group rather than individual experience in the choice of suitable refuges; and the ability to locate the same den year after year, transmitted from adults to the young that trail them. There may be some protective advantage against enemies when the snakes are congregated about the dens, since they seem able, possibly by movement, to transmit a sense of alarm to each other. For those that mate in the spring, the winter concentration is of definite value in providing mates. And finally, the balling up within the den, since it decreases the ratio of area to mass, has the advantage of conserving both moisture and heat. This latter point has been discussed at length with respect to *Storeria* and certain other harmless snakes by Noble and Clausen (1936, p. 271); see also Clausen (1936, p. 367) and C. H. Pope (1946, p. 6). Aggregation results in less moisture loss whether from skin or lungs, and there is a lower metabolic rate, which conserves energy in the form of fat.

I have discussed elsewhere (Klauber, 1937, p. 51) some statistical data on loss of weight by rattlesnakes during hibernation. It was my conclusion that adult rattlers going into hibernation in autumn are about 4 per cent heavier than when emerging in the spring. Juveniles lose somewhat over 20 per cent of their initial weight during hibernation. There is virtually no increase in length during hibernation.

A. M. Jackley was of the opinion that, with large population increases, den concentrations might become detrimental. Some inmates might be crowded out into only partly protected fissures; others might have their bodies fatally entangled. He found some individuals weak and emaciated when they issued from the dens, and thought some of the females carrying eggs into their second active season had suffered injury. It is possible that overcrowded dens may serve to limit population growth. Certainly hibernation is a season of hazard.

Woodbury and Harvey (1948, p. 181) have called attention to the different requirements that must be satisfied by hibernating dens in contrast with summer refuges. The latter, usually rock crevices or mammal holes, are more casual and fortuitous. Since they are only temporary refuges from heat and enemies, they may readily be abandoned any night should they prove unsuitable. But the winter den will prove a death trap should it be found untenable by reason of cold or moisture; for, once the snakes have entered and become immobilized by the winter temperature, it is too late to seek safety elsewhere. Hence the importance of the collective instinct that leads the annual retreat of an aggregation of rattlers to the same den year after year, once its suitability has been tested and proved by trial.

Summarizing the denning habits of the rattlesnakes, we may conclude that they are determined largely by the winter conditions that must be met, and, to a smaller degree, by normal habitat preferences. A long severe winter requires a den that rigidly adheres to certain essential qualities: it must furnish a space below the frost line, protected from the entrance of moisture and drafts. Since the requirements are severe, suitable dens may be hard to find and hence may

be widely separated. For this reason, the population per den is likely to be large, both because of the greater area from which the refugees are drawn and because of the necessary dependence on group experience. In milder climates, denning is more a matter of comfort than survival, and thus improvised refuges are the rule, for almost any rock crevice or mammal hole will suffice. But some differences in denning habits result from differences in summer habitats. For example, the timber rattler seeks appropriate dens amid the rock ledges that comprise its summer range; and, in the same severe climate, the massasauga finds its winter refuge in the swamps, wherein it passes its active life in summer.

Volsøe's studies of the hibernation of the European viper (1944, pp. 12-16) are of interest in showing many points of parallelism with the activities of rattlesnakes. Some items upon which his data are more complete and accurate than those available on rattlesnakes are as follows:

Vipers issue from hibernation on the first sunny days after the maximum temperature has reached 8° C. (46.4° F.).

Entrance into hibernation is less definitely fixed by temperature, but probably occurs when the maximum temperature sinks below 8° C. or possibly 9°-10° C. (48°-50° F.).

The average duration of hibernation in Denmark is 150 days.

Vipers do not "sleep" like hibernating mammals; they are merely in a state of low activity or torpidity because of the low temperature.

Cold winters may actually be more favorable than mild—provided a fatal temperature be not reached at the subterranean place of hibernation—since the reduced metabolism at the lower temperature involves less fat consumption.

Vipers probably cannot survive a body temperature lower than a few degrees below freezing.

#### SUMMER RANGES AND TERRITORIALITY

Closely related to the spacing of hibernating dens, and their repeated use by the same individuals year after year, are questions of the homing instinct, territoriality, and similar factors which have been shown to be of such importance in the lives of many birds and mammals. It is known that rattlesnakes disperse from their winter quarters and spread out through their summer ranges. Even if the average distance traveled be less than a mile, it will be obvious how scattered the summer population must be compared with the lying-out concentration at a den. At a den, the population may reach 1,000 rattlers, crowded within a space of less than an acre. If the same den represents the assemblage of the rattlers from a mile around, the population density in summer would be one rattlesnake on each 2 acres, which shows why summer snake collecting is so meager in yield compared with den raiding.

Homing instincts and summer prowling ranges can be ascertained only by the marking and repeated recapture of the snakes. The methods to be used in such researches have been described by Blanchard and Finster (1933, p. 344), Imler (1945, p. 271), Carlström and Edelstam (1946, p. 748), Stickel and Cope (1947, p. 128), Woodbury (1948, p. 127), Conant (1948, p. 1), Fitch (1949a, p. 514), Hillcourt (1950, p. 150), and Woodbury (1951, p. 5). The work of Woodbury and his associates (1951, p. 8) with Great Basin rattlesnakes (*C. v. lutosus*) has demonstrated that the same individual rattlesnakes do resort to the same den year after year, and hence show a homing instinct, as far as hibernation is concerned.

However, summer captures of marked snakes had not yet been made by Woodbury, so that the relationship of the den to the summer range was not established.

A. M. Jackley of Pierre, South Dakota, has thus described the dispersal of prairie rattlesnakes (*C. v. viridis*) from their winter refuges:

My studies indicate that in the spring, as a rule, the snakes leave the dens, which are located in buttes or ridges, in one general direction. Sometimes they go away for considerable distances before spreading out. I do not think this is the rule where they hibernate in prairie-dog towns, particularly if on level or gently rolling prairies. There are many cases where snakes are frequently encountered a mile or so to one side of the den, whereas they are rarely seen in the opposite direction. Naturally, these snakes cannot hunt collectively, for each one is on his own; nevertheless, they do gather where food is most plentiful and this accounts for considerable concentrations. The facts are that the areas infested with these snakes are so spotted that one cannot calculate the population, or determine their distribution in summer.

I have found in most localities that the rattlesnakes have what I call summer feeding grounds. This fact has often been observed where grain has been planted, which, of course, attracts mice and other rodents. Last year, as an example of this, a farmer put in 60 acres of oats, which was shocked and 30 days later was threshed. Eighty-odd snakes were killed when the grain was threshed. This is a little out of the ordinary in the way of a feeding-ground concentration, but it is a rule that within a mile or even more from a den, where a large colony hibernates, many of them will concentrate in favorable feeding areas. Oftentimes the feeding grounds may be within a mile of the den, but in other cases considerably farther. There isn't anything like an equal distribution over an area in the vicinity of a den.

Sweet (1954, p. 54) reports that in Montana the prairie rattlesnakes that have hibernated in limestone ledges, scatter for the summer over sage and hay meadows. Some writers have visualized a definite population movement during the summer, quite aside from the regular migrations to and from the winter dens. The timber rattler (*C. h. horridus*) is often stated to come down to the streams in the late summer, and a similar journey has been attributed to the prairie rattlesnake (*C. v. viridis*) in Montana (Mosimann and Rabb, 1952, p. 26). Further studies will be required to verify these habits. This phase of the problem, as affected by temperature, has been discussed elsewhere (pp. 430, 434).

Stephen H. Harwig of Pittsburgh made extensive studies of the activities of the timber rattlesnake (*C. h. horridus*) in western Pennsylvania. He observed them both at their dens during the lying-out periods in fall and spring, and also during their summer dispersal. Upon their habits in the latter season he had this to say:

May is the best time of year to hunt at the dens, but always the weather sets the pace. As a matter of fact, many snakes remain in the vicinity of some dens all summer, so that the take in May or September will only be 2 or 3 times as many rattlers as can be collected in the same places in June, July, or August. Some rattlers, particularly females, seem to stay at the dens all summer; especially is this true if the dens are only partly shaded and have a good low brush cover, chiefly huckleberry, with plenty of small mammals nearby.

In May and during favorable weather in June, July, and August, one may find a rattler or two every 200 to 1,000 feet on rocky hillsides in Cameron County, Pennsylvania; whereas in some other Pennsylvania areas you may find nothing in half a mile of fair-looking hillside, and then find 5 to 15 in a 10- to 50-foot stretch. They do not scatter evenly in summer. At some dens, I have seen greater concentrations in July and August than in the spring. Such summer gatherings apparently are not annual, but may occur by chance abetted by favorable temperature and food conditions.

I generally do not find a rattler in an entire season except in the rocky den country, although nearby residents and timber cutters find them elsewhere from June until about mid-September. Old stone walls, deserted farm buildings, sawdust and slab piles, are favorite summer resorts, as shed skins testify. Although it is probable that many rattlers stay along the streams in summer, the reports one hears tend to exaggerate their prevalence there because the fishermen and hunters also follow the streams. Woodcutters and berry pickers report plenty of rattlers on high dry flats, and in sunny clearings distant from streams. I have no information on how far rattlers range away from their dens in summer, but believe it to be 1 to 2 miles. Some are killed in farming country 3 to 5 miles from any known dens, but they may have found suitable individual winter refuges nearby.

Mr. Harwig has kindly supplied me with the statistics of his rattlesnake hunts in western Pennsylvania during the years of 1947 to 1953, inclusive. These hunts

TABLE 8:6  
OBSERVATIONS OF TIMBER RATTLESNAKES (*C. h. horridus*) BY  
STEPHEN H. HARWIG IN WESTERN PENNSYLVANIA, 1947-1953

Month	Sorties afoot	Miles afoot	Hours afoot	Rattle- snakes seen	Rattlers per mile	Rattlers per hour
April.....	12	20	21	8	0.40	0.38
May.....	68	182	193	212	1.16	1.10
June.....	44	113	120	66	0.58	0.55
July.....	34	101	109	72	0.71	0.61
August.....	42	101	118	86	0.85	0.73
September.....	73	174	183	157	0.90	0.86
October.....	12	36	37	4	0.11	0.11
Total or average.....	285	727	781	605	0.83	0.77

were made at or near the winter dens. The results are summarized in table 8:6 and indicate that the population peaks (in terms of rattlesnakes seen) are much less accentuated in the case of the timber rattlesnake (*C. h. horridus*) than the western rattlesnake (*C. viridis*) and its subspecies. No less than 285 separate sorties afoot, amid trees, underbrush, and rocks, are represented in this table. It is apparent that the timber rattler tends to concentrate in smaller numbers in winter, and remains closer to rocky hillsides in summer, than do the western forms subjected to similar climatic conditions.

MacQuarrie (1941, p. 83) believes that *horridus* in Wisconsin follows a regular course in going from one sunning or feeding spot to another in summer.

One problem that arises with respect to the summer activities of rattlesnakes is the extent to which they adhere to some summer operating headquarters—if, indeed, they have such a base of operations—and the space that they cover in their summer rambles in search of food. Do they exercise what is known as territoriality, that is, the defense of an area against other rattlesnake trespassers?

It is well known that many animals make a practice of defending a specific territory that they consider their own against the encroachments of others of their own species. This territoriality is sometimes established on a pair or family basis, sometimes as an individual claim. It is primarily for the purpose of staking a claim to all the suitable food within the area, but may be partly for the reser-

vation of refuges, nesting sites, or food storage. It is the common practice of such diverse creatures as coyotes and mice, hawks and humming birds, alligators and fence lizards.

Dixon (1937, p. 49) has shown how an area of many hundreds of square miles has been divided into a pattern of definitely outlined, contiguous plots, each used as a feeding range and defended by a single pair of golden eagles. He studied a complex of 27 of these plots that varied in size from 19 to 59 square miles, with an average of 36. In contrast, the territories claimed by smaller, slower-moving creatures may contain but a few hundred square feet.

W. H. Burt (1943, p. 346) distinguished between the home range of a creature and the defended territory, the latter being smaller. The home range is an area over which the animal may regularly wander, but which it may share with others; the defended territory is an inner core within which any trespass of its fellows will be opposed. When the term "territoriality" is used to indicate an objective exercised by an animal, it has reference to an active resistance to invasion.

Studies of how closely snakes adhere to specific areas are difficult to make because of the ophidian tendency to remain hidden much of the time. The best results have been attained with small snakes that take refuge under such things as boards, stones, or other flat objects, thus facilitating their recapture. Among the papers presenting appropriate data on snakes are those of Blanchard and Finster (1933, p. 334), Noble and Clausen (1936, p. 269), Blanchard (1937, p. 151), Imler (1945, p. 265), Seibert and Hagen (1947, p. 6), and Stickel and Cope (1947, p. 127). Although the evidence is not entirely consistent, the probability is that snakes do have home ranges. On the other hand, the tendency of snakes to aggregate, whether in winter dens or in more temporary summer refuges, makes it appear highly doubtful that there is any territorial defense.

So far, little work of this kind has been done on rattlesnakes. Mosauer (1933, p. 16) expressed doubt that the sidewinder had any regular range or even a permanent refuge, but thought rather that it traveled over the desert at random each night. One might travel as far as 2,000 feet in a single night (1935c, p. 22). Yet S. H. Walker, a professional snake collector operating in the sand dunes near Indian Wells, Riverside County, California, told Mosauer (1935b, p. 21) that each western diamond (*C. atrox*) had a more or less permanent refuge in a particular mesquite thicket. The snake would travel to and from this each night over a definite route from bush to bush, following almost the same course on its return, thus establishing a regular trail used repeatedly by the same snake. In one case a pair of rattlers traveled together over parallel tracks. Walker's observations tend to confirm adherence to a home range in this species.

Important studies of the prowling range and homing instincts of the northern Pacific rattlesnake (*C. v. oreganus*) were reported on by Horn and Fitch (1942, p. 121) and by Fitch (1949a, p. 539). Successive captures of 156 individuals taken a total of 359 times were recorded. The snakes were marked by clipping subcaudal scales so that each individual could be identified upon recapture (Fitch, 1949a, p. 514). As the winter temperatures are relatively mild on the San Joaquin Experimental Range where these studies were made, the rattlers did not congregate for winter hibernation, so that correlations between dens and summer ranges were

not established. However, the investigation did establish the following important facts regarding summer prowling:

- 1) There was much variation in the extent of travel. One snake moved  $\frac{1}{4}$  mile overnight, but most had much more limited orbits. There was a tendency to wander progressively farther from the point of first capture as more time elapsed.
- 2) Some individuals moved circuitously and by slow stages, using boulder piles or squirrel-burrow systems as focal points. But finally the snake would wander away, leaving this headquarters for others, more or less permanently. The successive headquarters were separated by only moderate distances. It could not be established whether there was a regular long-term route involving a return to the original center of operations, but probably there was no such return.
- 3) Of the 156 marked snakes recaptured, two had moved more than a mile, 14 others more than half a mile, and 14 others more than a quarter mile. The great majority, 126, had traveled less than a quarter mile, and 52 of these less than 100 yards. The time element involved in 121 of these recaptures varied from one month to 9 years. There was a definite lack of a wandering tendency; rather there was a disposition to remain within small areas. One rattler marked when a subadult, was found in the same rock pile 6 years and 14 days later.
- 4) The males ranged farther than the females.
- 5) Young tended to wander into new and more distant areas to a greater extent than adults.
- 6) There was a complete lack of any homing tendency in snakes released at some distance from the point of capture.

Although Fitch did not demonstrate the existence of a homing instinct, that is, a tendency to return when removed from an accustomed range, his results do indicate a definite territorial conservatism, that is a restriction of wandering or prowling to a relatively small area. There was no verification of Hudson's unsupported statement (1919, p. 22) that the homing instinct is strong in most snakes.

It is evident that where rattlers travel considerable distances to reach their dens, as is their practice in colder climates, the statistics of the distances traveled would be dependent on whether the marked snakes were repeatedly caught when concentrated at the dens, or when scattered over their summer ranges, or both.

From these somewhat inadequate data, we may conclude that rattlesnakes probably have home ranges, or at least favorite refuges to which they habitually or occasionally repair, but that they do not have a defended territory, from which other rattlers are driven away. The so-called male dance, a pattern of harmless and indecisive combat indulged in between male rattlesnakes, is interpreted as a sexual expression, rather than one of territoriality, and is discussed in chapter 10 on reproduction (p. 703).

#### ACCIDENTAL DISPERSAL. MIGRATION

In addition to the seasonal population movements just discussed, there may be forced or natural migrations over greater distances. Rattlers are known to swim readily (p. 496). They are quite buoyant and, because of their low rate of metabolism, are difficult to drown. It is to be supposed that many would survive a turbulent river-flood, even if there were no brush or debris upon which to ride. Thus there is little doubt that floods involve an important means of dispersal, as is evident from the following extracts from letters, as well as from published data. It is, however, to be noted that the involuntary colonists often find the new

habitat conditions unsuited to them and therefore a permanent range-extension is not established.

There are a few scattered rattlesnakes roundabout, but not many. Quite a few were found at a point two miles south of Grand Island, thought due to a river flood bringing them down from the west. *E. A. Toft, Grand Island, Nebr.*



Immediately after the flood of 1935 many rattlers were found along the Republican River. *F. N. Wiland, McCook, Nebr.*



Rattlesnakes have been reported here from time to time, but today there are very few, if any, in Saunders County. Early settlers say that they had killed them off before 1900. During the flood of the Republican River about fifty prairie rattlesnakes were reported; outside of these I haven't heard that any snakes of this species have been found near here. *S. Clay Coy, Wahoo, Nebr.*

H. S. Fitch (1936, p. 651) states:

At Gold Beach [Curry County, Oregon] I was told that rattlesnakes were not of regular occurrence there, but that several individuals found at different times evidently had been brought down the river on floating driftwood.

This is worthy of note since rattlesnakes do not normally occur in this coastal section of Oregon. Another report of the same kind is this:

We have had sporadic rattlesnake occurrences almost to the coast—evidently a migration enforced by a flood, or an accidental carry or stowaway. Such transients would not survive a coastal-slope winter—at least I do not believe they would—and must be considered accidental colonists, rather than permanent inhabitants. *Richard J. Grace, Portland, Oreg.*



Mr. Huber, our engineer, who formerly lived at Knights Landing in the Sacramento Valley, tells me that he observed rattlesnakes coming down on driftwood during flood stages of the Sacramento River. *Norman J. Farrell, U. S. Forest Service, Shasta, Calif.*

A similar condition was described in a newspaper item: "Colusa, Calif.—Following the first heavy rains of the season, numerous rattlesnakes, apparently caught by rising waters north of Redding, have floated down the Sacramento River on logs. Two or three rattlers are sometimes seen on one bit of floating debris."

Hallock (1905, p. 292) reported from San Diego County that rattlers could be seen—from bridges—floating seaward after severe spring floods. I heard the same stories at the time of the floods of 1916, when rattlers were reported in numbers in the debris at the mouth of the San Diego River. These floods, with little doubt, are the reason for the occasional presence of speckled rattlers (*C. m. pyrrhus*) along the coast in this county. They seem unable to obtain a permanent foothold here, their regular range beginning several miles back from the coast at about the 1,000-foot contour.

Wade (1900, p. 505) tells of a laborer in urban Pittsburgh who was bitten while working in a steel mill, the accident occurring in a district from which rattlers had long been absent. He concludes that the snake had been brought down the Allegheny River during a flood a few days before. Clench (1925, p. 40) records the case of an eastern diamondback drifting to Sanibel Island, Florida, on a floating island of water hyacinth, the trip involving some 27 miles. Dobie (1926,

p. 52) found no rattlers drowned when some flat land was flooded, and presumed that they had taken refuge in bushes and hummocks. Tixier (1940, p. 77, but written in 1844) said that rattlers were often seen swimming in the Mississippi River in times of flood, and that many were seen gathered as refugees on high ground.

Hurter (1911, p. 210), at West Prairie, Madison County, Illinois, during a season of high water along the Mississippi, collected 59 massasaugas (*S. c. catenatus*) in about two hours. The water was only three to six inches deep and the snakes had sought the high spots. Some seemed quite exhausted; evidently even this swamp-inhabiting form cannot swim for long periods. No doubt with swifter water or debris on which to find refuge, many would have been carried downstream for long distances.

That rattlers may be endangered if the temperature of the water is low enough to stiffen the muscles is evident from the following report:

Speaking of temperature reminds me of a question that has been puzzling me and on which I seem to find little information. Can a rattlesnake drown in cold water just because of the water's temperature? On three separate occasions, while traveling on the Red Deer River by boat, I have come upon rattlers which seemed to be drowning. They were turning over and over in the current and seemed most of the time to be on their backs. On all three occasions the water was cold. I saw one in June (in cold floodwater from the Rockies) and the other two in September when the water was cold because of the time of year. When taken out of the water these snakes seemed dull and stiff. They could move only very slowly. When dropped back into the water they were unable to keep their heads up and began to writhe slowly and stiffly as the current rolled them over and over. When taken out of the water and exposed to the warmth of the sun they became more active. Except for being stiff they seemed normal in every way.

On one of the occasions I had an urgent errand on the farther side of the river and left the rattlesnake in the bottom of the boat when I tied up. Before I left, it several times tried feebly to crawl up the side of the boat but failed miserably. When I returned about an hour later the snake was gone, so it had apparently regained enough strength to escape. *James W. Chapman, Empress, Alta.*

Another effect of water may be to drive, rather than carry, rattlers into new territory:

Several people have informed me that rattlesnakes are very common this year around Friant Dam where the backed-up water of this new reservoir has driven them out of the lowlands. *F. T. Scott, Visalia, Calif.*

A. M. Jackley found the following conditions at Fort Peck, Montana:

When the water rose in the reservoir, a considerable number of prairie rattlers took refuge in the face of the dam. This is a jagged mass of large blocks of granite and extends for over a mile. While not a suitable place for these snakes to winter, it was used as a last resort, and some of the snakes survived. The top of the dam is to be covered with another six feet of earth and gravel, and machinery is moving back and forth on top of the dam continually. The trouble is that some of these snakes are leaving the dam and coming into the town where there are many children. But there are comparatively few of them and they should soon be exterminated.

Menger (1903, p. 445) reported that, as a result of flood conditions in Texas, rattlers were carried into farms and pastures from which they had been absent for years.

Aside from the dispersal by floods, presumably the migration of snakes into new territories largely results from their seeking an increased food supply, a much slower type of dispersal than that produced by a flood. Sometimes they follow the rodents when these are increased by more suitable conditions resulting from irrigation.

I have caught or killed 14 rattlers within  $\frac{1}{4}$  mile of my house this season, where I had killed only two in the two years before. I suppose this is accounted for by their coming in either for water, or else following their food supply, which has moved closer to our irrigated fields. *H. O. Burton, Jacumba, Calif.*

Some people believe that bridges afford access to new territories, but this is to be considered highly doubtful. The following is an example of such supposition: "The general opinion is that rattlers will be seen north of the Missouri River here in Montana in a few years due to the auto bridge recently built."

Newspaper accounts occasionally report grass and forest fires as agencies of dispersal, the rattlers presumably being driven out of the devastated areas. This is to be doubted, as the snakes are too slow-moving and also could not know in what direction to flee. A few no doubt escape by taking to ground holes, and a shortage of food may later cause these to leave a devastated area.

That man and his accessories may be either a conscious or unconscious agency of dispersal is undoubtedly true:

Old-timers say that the only rattler ever found here was thought to have been brought in with a load of hay. *O. K. Thollehaug, Sisseton, S. Dak.*



I have known boys 10 miles west of Mandan, to be punished for catching rattlesnakes and bringing them into the city to set free. *Blair E. Seitz, Wahpeton, N. Dak.*

Vorhies (1928, p. 182) has discussed the confusing range records that have resulted when tourists have hauled animals about, and then, having tired of them, have released them far from their natural haunts. R. S. Palmer (1946, p. 3) mentions the finding of a frozen diamondback in Maine in December, evidently thrown from a passing automobile. This species does not occur naturally north of the Carolinas.

Others escape from zoos and circuses. T. E. B. Pope (1929, p. 167; 1930, p. 281; 1931, p. 327) has described in considerable detail the evidence as to the source of a colony of western diamond rattlesnakes (*C. atrox*) that became established 5 miles west of Viroqua, Vernon County, Wisconsin, far from the normal range of this species. It appeared that the snakes originally escaped from a circus in the vicinity of Pittsville, Wood County, sometime between 1923 and 1927. W. E. Dickinson, of the Milwaukee Public Museum, advised me, under date of May 25, 1945, that the fate of this colony was then somewhat uncertain. Two additional specimens had been killed; and as late as 1943 a newspaper report from Caledonia Township described the killing of a rattlesnake probably too large to have been a timber rattler. More recently (Nov. 16, 1953) Dickinson wrote me that the Vernon County colony had almost certainly died out, as there had been no further captures in the meantime. However there had been reports of diamondbacks, no doubt escapees, from Kenosha County, in the southeastern corner of the state.

Bryant (1915, p. 48) thought that the southern Pacific rattlesnakes on Santa Catalina Island, off the coast of southern California, were brought in by man, for the old-timers told him there had been none until hay was shipped in for domestic animals. The snakes were first seen around barns and then took to the hills. However, this is to be questioned, as a specimen was collected by Schumacher on Catalina as early as 1878 (Yarrow, 1883, p. 76), long before the time of which Bryant speaks. Besides, the island specimens show differences from those on the mainland, differences that are slight but that could not have become established in so short a time.

There is little doubt that the presence of one of the two subspecies of the western rattlesnake (*C. v. viridis* and *C. v. nuntius*) in the vicinity of the Hopi villages in northeastern Arizona, has resulted from the gathering of snakes for the snake dances over a rather wide area—they may be brought in by visiting Indians from a considerable distance—followed by their release after the ceremony. Only *nuntius* is native there.

Figuier (1869, p. 88) has stated that public exhibitions of rattlesnakes were at one time forbidden in France because of the fear that a pair might escape and start a colony. In 1940 the city of Berkeley, California, adopted an ordinance making it unlawful to keep or transport venomous reptiles in the city without a permit. This was enacted for the purpose of preventing the escape and colonization of dangerous snakes not already indigenous to the area. The northern Pacific rattler occurs naturally in the hills above the city.

Gadow (1930, p. 53), discussing the re-establishment of plants and animals in a district in Mexico, after devastation by the volcano Jorullo, stated that rattlesnakes had not been found there yet. He considers them slow migrants, not well suited for reinvasion. Although the devastated region would now afford an ideal ground for them, if they could get there, the broad belt of sand-smothered terrain to the west, north, and east has acted as an effective barrier, and it is now too well cultivated for them to cross. To the south, the mesas are difficult to ascend.



## 9. Food

### INTRODUCTION

To a large extent rattlesnakes feed on small mammals, particularly such rodents as mice, rats, prairie dogs, gophers, and ground squirrels. The adults of the larger species eat creatures as big as rabbits. Birds are not neglected, and at some seasons ground-nesting birds may constitute an appreciable part of the diet of some species. Lizards comprise a predominant part of the food supply of a few of the smaller species, and are quite important to the young of some of the larger kinds of rattlesnakes. Several species inhabiting a moist terrain live, at least to some extent, on such amphibians as frogs and toads. No vegetable food is ever eaten, except such as may be present in the digestive tract of the prey, or may be ingested by accident in the act of swallowing. There was long a belief, coming down from Aristotle (Cresswell, 1862, p. 204) that snakes eat vegetable food, but this was never extensively believed to be true of rattlesnakes.

The several rattlesnake species, because of their differences in size and the variations in the kinds of animals available to them, differ considerably in their normal diets; therefore, to avoid repetition, I shall largely restrict the mention of particular items of diet to lists segregated by species or subspecies. However, brief summaries will first be presented to give some indication of the scope of the diet of the two genera, particularly to make available in one place some of the more unusual food items that have been recorded. This involves some repetition, first, under kinds of food, and then under the several species of rattlesnakes.

### KINDS OF FOOD

#### MAMMALS

It is probable that every species of mammal living in the same territory with some kind of rattlesnake, provided it is small enough to be swallowed, occasionally falls prey to these snakes. Even if the adults are too large, the young may form a regular part of the diet. For a hungry rattler, with his death-dealing fangs, can quickly subdue even so fierce and bloodthirsty a fighter as a mink or weasel, although such carnivores are not regularly eaten.

Because of their convenient size and population density, it is probable that the following genera of rodents comprise the bulk of the food supply of rattlesnakes: White-footed mice (*Peromyscus*), pocket mice (*Perognathus*), grasshopper mice (*Onychomys*), meadow mice (*Microtus*), harvest mice (*Reithrodontomys*), kangaroo rats (*Dipodomys*), wood rats (*Neotoma*), and chipmunks (*Tamias* and *Eutamias*). To these there may be added, as important elements in the food supply of the larger rattlesnake species, prairie dogs (*Cynomys*), ground squirrels (*Citellus* and related genera), squirrels (*Sciurus*), and cottontail rabbits (*Sylvilagus*), the young of these larger mammals being particularly subject to predation.

Surface (1906, p. 196) found, in Pennsylvania, that 94 per cent of the food of the timber rattlesnake (*C. h. horridus*) was made up of mammals. In Virginia, Uhler, Cottam, and Clarke (1939, p. 609), studying the same species, determined the mammal percentage to be almost 87. Fitch and Twining (1946, p. 70), in their detailed investigation of the food habits of the northern Pacific rattler (*C. v. oregonus*) in Madera County, California, ascertained that 85 per cent of the items found in the rattlesnake stomachs were mammals, while nearly 88 per cent of the scats contained mammal remains. Fitch (1949a, p. 548) translated these data into weights, and concluded that mammals comprise 97.9 per cent of the food in terms of bulk. It is probable that, in the United States, mammals comprise from 80 to 98 per cent of the food of the adult rattlesnakes of all species except the sidewinder (*C. cerastes*), the rock rattlesnake (*C. lepidus*), the Arizona twin-spotted rattler (*C. p. pricei*), the ridge-nosed rattler (*C. w. willardi*), and the pigmy rattlers and massasaugas of the genus *Sistrurus*, all of which—except the eastern massasauga *S. c. catenatus*—are characterized by a relatively small size. Although these small rattlesnakes live to some extent on mammals, lizards comprise a greater part of their diets than is the case with the larger species.

The fact that small mammals, especially rodents and lagomorphs (rabbits and hares), comprise the bulk of the food supply of the larger rattlesnake species, and an important part of the diet of the smaller, will be fully apparent from the prey lists under the several species. They are suitable in size and are usually plentiful in the areas where rattlesnakes occur. Estimates of populations per acre of some of these small herbivorous mammals have been presented by Mohr (1947, p. 223; see also Fitch, 1949a, p. 570), from whose summaries one may gain some idea of the vast food supply that these small creatures offer predators; for we learn that the populations often run from 10 to 50 per acre, and in some instances exceed 100. These figures explain the surprising numbers that are sometimes illuminated by a car's headlights, as they skitter across the road at night.

It is to be expected that most pit vipers, including the rattlesnakes, should feed on warm-blooded prey, since they have a special sense organ—the facial pit—to facilitate its detection; for the pit, as true a sense organ as an eye or ear, serves to locate any object having a somewhat higher temperature than its surroundings.

The method by which rattlesnakes generally seek their food—that is, by lying in wait for and lunging at passing creatures—coupled with a not especially acute sense of vision, occasionally results in their eating creatures quite different from their customary prey. A few unusual mammals have been reported. For example, Kalm (1752–53, p. 59) stated that the timber rattler occasionally ate minks. Frank E. Brink of Milford, Pennsylvania, wrote me that he had known timber rattlers to

eat minks and weasels; W. E. Fulmer, of Lehigh, Pennsylvania, found a *horridus* that had eaten a weasel;<sup>1</sup> and J. W. Crigger, of Huntersville, West Virginia, mentioned weasels among their prey. I noted a red diamond rattlesnake (*C. r. ruber*) from Jamul, California, that contained a young skunk (*Spilogale gracilis microrhina*). Hall (1951, p. 200) reported that a rattler (species undesignated) at Banning, California, contained the skull of a long-tailed weasel (*Mustela frenata latirostra*). There is no doubt that small carnivores are occasionally eaten, although not a regular part of the diet.

Audubon and Bachman (1854, vol. 2, p. 116) have reported two instances in which half-grown opossums were devoured. Uhler, Cottam, and Clarke (1939, p. 610) found the remains of a bat in the stomach of a timber rattler; and there are other records of bats being eaten. C. Whitman of Madera, California, found a northern Pacific rattlesnake crawling along a dead tree that formed a bridge to a large rock in the Fresno River. There was a bat roost in a crack of the rock, and Mr. Whitman was convinced that the snake was seeking the bats.

As to the maximum size of prey, Davenport (1943, p. 107) states that a large western diamond (*C. atrox*) can eat a full-grown jackrabbit, and one of my correspondents has voiced the same opinion, but I think this needs confirmation. Certainly adult diamondbacks can swallow a full-grown cottontail.

#### BIRDS AND EGGS

Birds comprise an appreciable part of the diet of many rattlesnakes, particularly those that live in areas where ground-nesting birds are plentiful. The fact that nearly all kinds of rattlesnakes eat birds occasionally will be manifest from the food lists set forth under each species. Uhler, Cottam, and Clarke (1939, p. 609) found that birds formed about 13 per cent of the food of the timber rattlesnake (*C. h. horridus*) in the George Washington National Forest. Fitch and Twining (1946, p. 70) reported that birds comprised only 2 per cent of the food items of the northern Pacific rattlesnake (*C. v. oregonus*) in Madera County, California. Fitch later (1949a, p. 548) reduced this to less than 1 per cent by weight. It is probable that the prairie rattlesnake (*C. v. viridis*) feeds on birds to a considerable extent, to judge by the number of confirmatory reports from its range, where ground-nesting birds predominate. In captivity, many species of rattlesnakes readily eat birds.

Rattlers can become a nuisance around breeding farms where game birds are raised, although, since they do not excel as fence climbers, they are not nearly so troublesome as some of the harmless snakes, such as the gopher snakes (*Pituophis*), king snakes (*Lampropeltis*), and racers (*Masticophis*). It is doubtful whether rattlesnakes can be considered one of the important predators of wild game birds in any area; they have not been shown to be so in any of the really adequate studies of game birds thus far completed.

Rattlesnakes will kill and eat young chickens and turkeys, and several of my correspondents have included poultry in their lists of rattler foods. Nevertheless, the farmers with whom I have consulted have not indicated that rattlers are thought to be important threats to their flocks, for there are, in every area, other predators much more destructive.

<sup>1</sup> *Pennsylvania Game News*, vol. 29, no. 10, p. 24, Oct., 1953.

Rattlesnakes occasionally eat eggs, but to a lesser extent than some of the other large snakes, such as those already mentioned. In fact, egg-eating is sufficiently rare to warrant the gathering of the data for all species here, rather than under the individual species.

Brons (1882, p. 585) reported that the prairie rattlesnakes (*C. v. viridis*) ate the nestlings and eggs of the burrowing owls with which they were supposed to live in harmony. Bent (1932, p. 76) quoted Frank Willard's report that he had been watching the nest of a Gambel quail (*Lophortyx gambeli gambeli*) for some days. It contained 18 eggs. Later he found a rattlesnake coiled around the eggs, two of which were gone. The female quail was fluttering overhead, with the rattler striking at her. Unfortunately, Willard did not open the snake to see if it had eaten the eggs; Gorsuch (1934, p. 74) doubts that they were taken by the snake. Glading (1938, p. 336) found a coiled northern Pacific rattler (*C. v. oreganus*) resting on the eggs in the nest of a California valley quail. It was assumed that the snake had eaten some of the eggs, but when the snake was killed the stomach was found to be empty. Glading concluded that quail eggs are not a part of the regular diet of this snake.

Storer, Cronemiller, Horn, and Glading (1942, p. 134), continuing the same studies at the San Joaquin Experimental Range in Madera County, California, stated that while 30 per cent of the quail nests were destroyed by predators, and although rattlers far outnumbered all other snakes in the area, the rattlers could not be charged with damage to the nests. Other snakes—gopher and king snakes especially—although fewer in numbers than the rattlers, were much more destructive predators. Blakey (1934, p. 13), working on the Missouri Ozark Range, reported that the timber rattler was fond of wild-turkey eggs, but he seems to have based this conclusion on finding a single individual that had eaten four. Mosby and Handly (1943, p. 128) were unable to verify this type of predation in Virginia and concluded that the timber rattler is not a serious menace to wild turkeys. Flack (1866, p. 332) reported that turkey eggs were eaten by rattlers in Texas.

Uhler, Cottam, and Clarke (1939, p. 608) mention birds' eggs found in the stomachs of timber rattlers (*C. h. horridus*). Boone (1937, p. 54) told how a "yellow Pacific rattlesnake"—probably a Mojave rattler (*C. s. scutulatus*)—climbed five feet into a mesquite tree and robbed a bird's nest of its eggs; however, the rest of the paper is so inaccurate as to invite skepticism regarding this episode. Rutledge (1936, p. 139) found an eastern diamond rattlesnake (*C. adamanteus*) in a woodpecker's hole. Upon examination, the snake was found to contain the mother woodpecker and five eggs.

A number of my own correspondents have reported the eating of eggs by rattlers. F. R. Cochran, U. S. Forest Service, Sundance, Wyoming, discovered a prairie rattlesnake (*C. v. viridis*) in his hen house; the stomach, opened because of a suspicious bulge, was found to contain an unbroken hen's egg. A similar report was made by Fred W. Barnes, U. S. Fish and Wildlife Service, Hines, Oregon, of a hen's egg found in a Great Basin rattler (*C. v. lutosus*). Charles G. Holzworth, Kremmling, Colorado, wrote me that prairie rattlers (*C. v. viridis*) eat the eggs of ground-nesting birds as well as the young; and Clarence R. Ousley, of Napa, California, gave similar information regarding the northern Pacific rattlesnake (*C. v. oreganus*). William Anderson, Reynolds Creek Ranger Station, near Globe, Arizona, saw a yellowish rattlesnake (*C. atrox* ?) that had eaten the eggs found in a robin's or

thrush's nest some 10 feet above the ground. It was not stated whether an examination was made of the stomach contents to prove that eggs, rather than young birds, had been eaten. Attacks that were being made on the rattler by the parent birds, indicated that the nest had been robbed of something. Bruce Centerwall reported finding what he thought were the shells of quail eggs in a western diamond rattler (*C. atrox*). W. W. Britton of Chambersburg, Pennsylvania, includes grouse eggs among the food items of the timber rattler (*C. h. horridus*).

I think we may conclude that eggs are occasionally eaten by some species, but certainly they form only a minor part of the rattlesnake diet.

#### REPTILES

To a considerable degree, lizards comprise one of the normal food items of rattlesnakes. This is especially true in the Southwest, where lizards are plentiful, and it is also characteristic of particular rattlesnake species. The smaller rattlesnakes are habitual lizard eaters, since the attenuated form of the lizard allows it to be more easily swallowed than a mammal, which is thicker-set for the same bulk. Thus the young of the small species of rattlers—*pricei* and *lepidus* for example—find many lizards running about that they can swallow, while mice within their capacity would be found only in a nest of hairless young within a few days of birth. This is one of the reasons why the smaller rattlesnake species are confined to areas with adequate lizard populations. The adults of some of the small species continue to prefer lizards even after they have attained such a size that they could readily eat adult mice.

Not only are the small kinds of rattlesnakes dependent on lizards, but the young of the larger species regularly eat them, and they are not completely scorned by the adults. However, studies have shown (e.g., Klauber 1944, p. 116, on sidewinders) that there is a trend from lizards toward mammals as a basic diet, as the snakes age and thus grow to a size such that mammals within their swallowing capacity are more plentiful. C. B. Perkins, when collecting prairie rattlesnakes (*C. v. viridis*) at hibernating time in the late fall, noted that the juvenile rattlers with only a button regurgitated lizards, while the youngsters that had achieved an additional rattle or two had eaten small mice.

Uhler, Cottam, and Clarke (1939, p. 609) found no lizards in the stomachs of the 141 timber rattlesnakes (*C. horridus*) that they examined. In their studies of the northern Pacific rattlesnake on the San Joaquin Experimental Range, Fitch and Twining (1946, p. 70) determined that lizards made up 10.4 per cent of the prey items found in the stomach examinations and 7.8 per cent in the scats. It is probable that these figures are somewhat on the low side, as lizard scales are more affected by digestion and therefore less easily recognized than mammal hair. These same authors conclude that a lack of lizards—for they are not plentiful on the Range—is one of the factors limiting the rattler population; the young are unable to find sufficient food and many starve to death, although an adequate supply of mammals is available for the adults (p. 69). Horned toads are often fatal to rattlesnakes that try to eat them, as mentioned elsewhere (p. 660).

Other reptiles are rarely eaten; they do not constitute a normal item of diet as do lizards. W. (1846, p. 63) threw a small land tortoise into a rattler's cage. It disappeared and he assumed it had been eaten, but this is to be doubted. Rarely will

a rattlesnake eat another snake. W. T. Sherman of Silver City, New Mexico, wrote me that he found a 3-foot rattler in the act of swallowing an 18-inch bull snake. One of the timber rattlesnakes examined by Surface (1906, p. 196) contained the remains of a snake, but Uhler, Cottam, and Clarke found none in their series. J. W. Crigger wrote me that a timber rattler (*C. h. horridus*) had eaten a pine snake; and R. J. McCormack of South Pittsburg, Tennessee, also mentioned one that had been swallowed by the same species. Shorey (1953, p. 25) says that timber rattlers sometimes eat small snakes. E. H. Mortensen stated that a captive northern Pacific rattler (*C. v. oregonus*) ate a king snake. Milstead, Mecham, and McClintock (1950, p. 557) found a western hook-nosed snake (*Gyalopion canum*) in the stomach of a mottled rock rattler (*C. l. lepidus*).

Halter (1915, p. 60) reported that a pigmy rattler (*S. miliarius*) in captivity ate a garter snake (*Thamnophis sirtalis*) longer than itself. Paul L. Swanson wrote me that a southeastern pigmy rattlesnake (*S. m. barbouri*) disgorged a Florida ribbon snake (*Thamnophis sauritus sackeni*). The ribbon snake had probably been eaten in captivity. Allen and Neill (1950b, p. 11) say that *S. m. barbouri* eats ribbon snakes, young water snakes, and occasionally the young of its own species. Conant (1951, p. 255) found the remains of a small snake, probably *Storeria dekayi*, in an eastern massasauga (*Sistrurus c. catenatus*). There are old reports (Anon., 1838, p. 72; Martin, 1851, p. 251) to the effect that rattlesnakes occasionally eat water moccasins, but these require confirmation.

In captivity, rattlesnakes are occasionally cannibalistic, a result that may happen when two rattlesnakes start to eat the same mammal. When this occurs, one is quite likely to swallow the other, the swallower being the larger, or, if about the same size, the one which, in advancing its jaws along the prey, happens to take the first bite that puts its upper jaw over the edge of the cage-mate's. This danger is well known in zoos, and therefore care is taken, in feeding, not to permit two snakes to seize the same animal.

Sometimes cannibalism among captive snakes is not the result of two snakes seeking the same prey. At the San Diego Zoo, one prairie rattler (*C. v. viridis*) ate another that had been a cage-mate for several years. Both were adults and of similar size. The meal proved too large and was regurgitated. In another instance a red diamond rattlesnake (*C. r. ruber*) ate a southern Pacific (*C. v. helleri*); and in another a southern Pacific ate a 30-inch speckled rattler (*C. m. pyrrhus*). A western diamond (*C. atrox*) ate a blacktail (*C. m. molossus*) that may have died just before it was eaten.

Sometimes one rattler will eat another when they are crowded together in a shipping container, as happened when one ate another in a shipment of juvenile western diamonds (*C. atrox*). Hathcock (1937, p. 339) has shown a photograph of one northern Pacific rattlesnake swallowing a cage-mate of somewhat smaller size. This occurred when they were crowded and hungry.

C. J. C. (1933, p. 59) wrote of one prairie rattlesnake (*C. v. viridis*) that had swallowed another two-thirds of its own length. The snake that had this meal was found in the wild, and therefore this was not an instance of cannibalism among captive snakes. However, the author admits that the swallowed snake might have been found dead by the other. Gloyd (1933, p. 98) reported a further case of a prairie rattler that disgorged another it had eaten in the wild. In this instance

there was evidence that the swallowed snake had been found dead, for it seemed to be headless—although the head may have been completely digested—and some rattlers had lately been killed at the den where the swallower was found. Ruthven (1911, p. 270; Ruthven *et al.*, 1912, p. 126; 1928, p. 132) reported two instances in which a massasauga (*S. c. catenatus*) had eaten snakes, one of which was another rattler of the same species. Both snakes had evidently been dead for a considerable time before they were eaten.

We may conclude that cannibalism among rattlesnakes in the wild is quite unusual; and, in the rare instances when it has occurred, the snake eaten has sometimes been dead before it was swallowed.

#### AMPHIBIANS

It is probable that all species of rattlesnakes occasionally eat frogs or toads. To several species inhabiting humid areas, they constitute a more important source of food than lizards. Probably the most consistent amphibian eaters are the rattlers of the genus *Sistrurus*—the massasauga (*S. catenatus*) and the pigmy rattler (*S. miliarius*). To judge from published records and the reports of my correspondents, the list of the subspecies of rattlesnakes that eat amphibians, at least occasionally, includes the following: The prairie rattlesnake (*C. v. viridis*), Great Basin (*C. v. lutosus*), northern Pacific (*C. v. oreganus*), southern Pacific (*C. v. helleri*), timber (*C. h. horridus*), canebrake (*C. h. atricaudatus*), eastern massasauga (*S. c. catenatus*), and the several subspecies of the pigmy rattlesnake (*S. miliarius*). Falck (1940, p. 135) reported that the mottled rock rattlesnake (*C. l. lepidus*) would eat not only frogs in captivity but tiger salamanders as well. However, it refused a newt (*Triturus*). A small dusky rattlesnake (*C. t. triseriatus*) was found to have eaten a salamander.

#### FISHES

Two of my correspondents have mentioned fishes as rattlesnake food. One claimed to have seen a prairie rattlesnake (*C. v. viridis*) in the act of eating a trout about eight inches long; the other observed a western pigmy rattlesnake (*S. m. streckeri*) catching small minnows in a shallow slough. Evermann and Clark (1914, p. 348) expressed the opinion that the massasauga (*S. c. catenatus*) probably eats fish. Drake (1921, p. 50) reported that northern Pacific rattlers (*C. v. oreganus*) catch salmon trout, and Shorey (1953, p. 25) included small fishes in the diet of the timber rattlesnake (*C. h. horridus*). These reports require confirmation.

#### ARTHROPODS

Insects and other arthropods are rather frequently mentioned as being among the creatures eaten by rattlesnakes. Of a few of the records there can be no question; but, as to most of the others, it is probable that the insects were ingested as the stomach contents of other prey such as lizards and toads, and then outlasted their original captors during the digestive process in the rattlesnake. It is significant that insect remains are most frequently found when there are lizard scales in the food residue.

Surface (1906, p. 191) states that the eastern massasauga (*S. c. catenatus*) probably eats insects such as grasshoppers, but this is doubted by Atkinson and Netting

(1927, p. 42). Evermann and Clark (1914, p. 348) include crawfish in the menu of this subspecies. Neither Surface (1906, p. 195), nor Uhler, Cottam, and Clarke (1939, p. 609) list insects among the stomach contents of the timber rattlesnake (*C. h. horridus*), although several early writers (e.g., Dudley, 1723, p. 294; Pennant, 1787, p. 88) reported that insects were eaten. Messeling (1953, p. 21) claimed that he watched young timber rattlers catching flies and that they seldom missed.

Wright and Bishop (1915, p. 189) found "the remains of several beetles, grasshoppers, spiders, and the ribs and pieces of skin of a very small snake or lizard" in a pigmy rattler (*S. miliarius*). Mitchell (1903, p. 31) and Conant and Bridges (1939, p. 143) also mention insects as having been eaten by this species. Centipedes likewise are eaten (Hamilton and Pollack, 1955, p. 3).

I have had a number of reports to the effect that prairie rattlesnakes (*C. v. viridis*) and Great Basin rattlesnakes (*C. v. lutosus*) eat Mormon crickets, which at times are exceedingly abundant. Most of these merely listed the crickets among the food items of which the rattlesnakes partake, but the following is more evidential:

Once I saw Mormon crickets being eaten by an adult rattlesnake. It had one about swallowed when I came upon it. There were numerous snakes along the road among the large band of the crickets; the others could have eaten them, also, but I didn't have the time to open them up to examine them. I don't know if they would take them from choice or if their abundant proximity irritated this one into trying it. *C. H. McDonald, U. S. Forest Service, Stevensville, Mont.*

Lawrence Kelly of Harper, Oregon, reported grasshoppers and crickets among the stomach contents of northern Pacific rattlesnakes (*C. v. oregonus*); and Von Bloeker (1942, p. 38) found three Jerusalem crickets in the stomach of a southern Pacific (*C. v. helleri*). However, this snake also contained a toad that may have eaten the crickets first. A Queretaran dusky rattlesnake (*C. t. aquilus*) was found to contain a cricket, probably of the family Gryllidae. Hermann (1950, p. 392) reported that western diamond rattlers (*C. atrox*) feed on lubber grasshoppers (*Brachystola magna*). Stomach analyses showed these insects to have been a regular part of the diet of the rattlers at that time and place.

I examined a Mojave rattlesnake (*C. s. scutulatus*) that contained the remains of a centipede and what appeared to be insects. I once found a caterpillar in the stomach of a sidewinder, but it also contained a fringe-footed sand lizard (*Uma*) that may have been eating the caterpillar when seized by the rattler. I was told by a youngster who kept a brood of captive sidewinders that they ate meal worms; however, he had not dissected them to make sure the meal worms had not escaped from the cage, as they often do. Kauffeld (1943b, p. 609) states that young specimens of *klauberi* and *pricei* in captivity refused meal worms, small grasshoppers, and earthworms.

#### VEGETABLE AND MINERAL FOODS

No snake eats vegetable food,<sup>2</sup> but occasionally small bits of vegetation, such as leaves, twigs, or sticks, are found in the intestinal tract, swallowed by accident or ingested with prey that had fed on vegetable matter. I noted a cocklebur in the throat of a prairie rattlesnake (*C. v. viridis*), a sumac leaf in the intestinal tract of

<sup>2</sup> Evidence has recently been cited indicating that the African egg-eating snake (*Dasypeltis*) eats certain fruits (Irvine, 1953, p. 173, and other references cited thereunder).

a red diamond (*C. r. ruber*), and another leaf in a sidewinder (*C. cerastes*). A Central American rattlesnake (*C. d. durissus*) contained a kernel of corn, together with feathers suggesting its probable origin.

I have found gravel in one southern Pacific rattlesnake (*C. v. helleri*), and a small stone in a Coronado Island rattlesnake (*C. v. caliginis*). Ruthven (1907, p. 593) reported a stone 14 mm. in diameter in the stomach of a western diamond (*C. atrox*). When a rattlesnake is observed scraping prey on the ground to dislodge it, when it has become caught in the angle of the jaw while being swallowed, we can readily see how such foreign material may be ingested. It is not unusual to find coarse sand in the lower intestinal tract of rattlers.

### SPECIES PREFERENCES

I shall now present such data as are available on the known food preferences of the several species and subspecies of rattlesnakes. The data are presented in the alphabetical order of the technical names, first by species, then by subspecies under each species.

*Eastern Diamond Rattlesnake* (*C. adamanteus*).—This is the largest of rattlesnakes. An adult has no difficulty in eating a mammal as large as full-grown cottontail rabbit. Even juveniles can swallow adult mice, and therefore seldom resort to slimmer creatures like lizards, upon which the smaller species of rattlers must depend. Birds are sometimes eaten by diamondbacks. Rabbits, squirrels, and birds are mentioned as the principal foods of this species by Davis and Brimley (1944, p. 9). Allen and Neill (1950a, p. 11) say that adult eastern diamondbacks feed mainly on rabbits, along with some rats, mice, squirrels, towhees, and quail.

Barbour (1920, p. 57; see also Carr, 1940, p. 96) tells of finding a king rail in the stomach of a large Florida diamondback. Stoddard (1942, p. 219) reports two instances wherein bobwhites were eaten. Davis (1949, p. 283) mentions a large diamondback that had eaten a young wild turkey. Rutledge (1936, p. 138) states that diamondbacks eat quail; he also claims to have found one in a pileated woodpecker's nest, after the mother bird and four eggs had been eaten by the snake. Hudgens (1953, p. 48) found a big diamondback that was swallowing a quail.

Williams (1892, p. 345) found that the diamondback, when in captivity, preferred birds to rats and mice. Allen and Slatten (1945, p. 26) were told that, on Cudjoy Key, off Key West, *adamanteus* fed on rats and birds, rabbits being quite scarce. But in most areas the Florida and eastern cottontails (*Sylvilagus f. floridanus* and *S. f. mallurus*) and the marsh rabbits (*S. p. palustris* and *S. p. paludicola*) are the mainstays of the adult diamondbacks.

*Western Diamond Rattlesnake* (*C. atrox*).—This large rattlesnake is primarily a mammal feeder, a full-grown snake having no great difficulty in swallowing an adult cottontail. In fact, Menger (1905, p. 27) was told that one ate a full-grown jackrabbit; and J. D. Bankston of Mason, Texas, has written me of finding a western diamond 64 inches long and weighing eight pounds, that contained a partly digested rabbit which seemed to him to be a full-grown jack. Another report mentioned the finding of a jackrabbit's ear in the stomach of an *atrox*. I think the

ability of *atrox* to swallow a full-grown jack requires confirmation. Birds and lizards are occasionally eaten, the latter especially by the young snakes. In a series of *C. atrox*, 14 specimens contained mammal remains, compared with 2 that had eaten lizards.

The following reports on the food habits of the western diamondback have been sent me by correspondents:

In July 1936 in Walker County, Texas, in the Trinity River bottom land, I saw a large diamondback rattlesnake with a fox squirrel nearly half swallowed. I was making a study of the fox squirrel at the time and I estimated that the squirrel was an adult, weighing about one pound. *Phil Goodrum, Atlanta, Ga.*



While I was on the Aransas National Wildlife Refuge, Texas, a very large (about seven-foot) diamondback rattler was brought in from a nearby peninsula. I removed a swamp rabbit (*Silvilagus a. aquaticus*) from the stomach. *Arthur F. Halloran, Fish and Wildlife Service, Yuma, Ariz.*



In examining the stomach contents of western diamond rattlers, I have found small mammals such as ground squirrels, young rabbits, and field mice; also birds (thought to be young quail), egg shells (presumably quail), and what looked like a part of a toad, but may have been a large lizard. *P. Bruce Centerwall, U. S. Forest Service, Tonto Basin, Ariz.*



I have twice found Merriam's pocket mice (*Perognathus m. merriami*) in western diamond rattlers, and a spiny pocket mouse (*P. h. hispidus*) in another. A small chicken was found in one. I was told of one that swallowed a full-grown cottontail. *A. J. Kirn, Somerset, Tex.*



I have one record of a *Crotalus atrox* found dead on the road three miles southwest of Tucson, Arizona, with an adult pocket mouse (*Perognathus f. flavus*) in its mouth. This snake either disgorged the pocket mouse when run over by a car or was in the process of eating it when killed. *Lee W. Arnold, Fish and Wildlife Service, Denver, Colo.*

The following are some of the items of mammal prey mentioned in the literature: Mitchell (1903, p. 37)—fox squirrel, Texas; Ruthven (1907, p. 593)—full-grown ground squirrel, Arizona; Anon. (1938a, p. 166)—full-grown cottontail, Oklahoma; Huey (1942, p. 375)—Bailey pocket mouse (*Perognathus b. baileyi*), Arizona; Hermann (1950, p. 392; Milstead, Mecham, and McClintock, 1950, p. 557)—another pocket mouse (*P. merriami*), Texas; Marr (1944, p. 488)—young cottontails (*Sylvilagus auduboni*) and white-footed mouse (*Peromyscus maniculatus* or *P. leucopus*), Texas; Woodin (1953, p. 294)—grasshopper mouse (*Onychomys torridus*), Arizona; Blair (1954, p. 241)—little short-tailed shrew (*Cryptotis p. parva*), Texas. Vorhies and Taylor fed *atrox* with wood rats (*Neotoma a. albigula*). No doubt they eat them in the wild.

As to birds, Mitchell (1903, p. 37) claimed to have twice seen mockingbirds eaten. Anon. (1938a, p. 166) reported from the Wichita Mountains, Oklahoma, a 56-inch western diamond that had swallowed a quail, besides a full-grown cottontail. Jackson (1942, p. 11A) killed a three-and-a-half-foot rattler, probably of this species, that had swallowed a nearly full-grown Gambel's quail. Bell (1932, p. 225), about the year 1854, examined a rattler (probably of this species) that had swallowed a burrowing owl. Milstead, Mecham, and McClintock (1950, p. 557) found unidentified birds in two western diamonds.

As to reptiles, Woodbury and Woodbury (1944, p. 372) reported that a young specimen from Oaxaca, Mexico, had eaten a whiptail lizard (*Cnemidophorus*). McCallion (1945, p. 198) states that young specimens ate scaly lizards (*Sceloporus*) in captivity. Milstead, Mecham, and McClintock (1950, p. 557) found a scaly lizard and a Texas banded gecko (*Coleonyx brevis*) in *atrox* stomachs.

Hermann (1950, p. 392) has reported that western diamond rattlers feed on lubber grasshoppers (*Brachystola magna*). I have seen the remains of three insect orders—grasshoppers, beetles, and ants—in the stomach of a single *atrox*. But it also contained mammal hair and the skin of an iguanid lizard, and probably the insects had been contained in the lizard or mammal when they were eaten by the rattler.

*Mexican West-Coast Rattlesnake* (*C. b. basiliscus*).—Seven specimens contained mammal (probably rodent) hair. No data are available on the food habits of the subspecies *C. b. oaxacus*.

*Mojave Desert Sidewinder* (*C. c. cerastes*).—Sidewinders live largely on lizards and small mammals, the smaller snakes favoring lizards, with an increasing preference for small mammals as they age (Klauber, 1944, p. 116). I have examined specimens that contained whiptail lizards (*Cnemidophorus tigris*) and pocket mice (*Perognathus*). One sidewinder of this subspecies contained both lizard scales and mammal hair; another had the remains of a bird. Merriam (in Stejneger, 1893, p. 217) mentioned specimens that had eaten pocket mice and kangaroo rats (*Dipodomys*). Woodbury (1931, p. 113) also had a specimen that had eaten a whiptail lizard. Van Denburgh (1922, p. 957) mentions a sidewinder that had eaten a desert horned toad (*Phrynosoma platyrhinos*) with fatal results because of the sharp horns; I am uncertain to which subspecies the snake belonged. Although the sidewinder is primarily a night feeder—it is, in fact, the most consistently nocturnal of all rattlesnakes—H. T. Woodall found one that was eating a whiptail lizard above ground at midday. This was at Twentynine Palms, San Bernardino County, California.

*Sonoran Desert Sidewinder* (*C. c. cercobombus*).—Intestinal remains show this subspecies to subsist on lizards and rodents.

*Colorado Desert Sidewinder* (*C. c. laterorepens*).—Like the other subspecies, this sidewinder lives on small mammals and lizards. Lizards, because of their elongated form, are particularly important to the younger snakes, for there are few mammals small enough for a juvenile sidewinder to eat. I found that 13 specimens that had eaten mammals averaged 457 mm. in length (range 324 to 606 mm.), while 10 that contained lizards averaged 341 mm. (range 260 to 543 mm.). The lizards that were recognizable were desert side-blotch lizards (*Uta stansburiana stejnegeri*), fringe-toed sand lizards (*Uma n. notata* and *Uma inornata*), gridiron-tailed lizards (*Callisaurus draconoides gabbi*), and desert whiptails (*Cnemidophorus t. tigris*). Among the mammals eaten were pocket mice and kangaroo rats. C. B. Perkins and I found a sidewinder of this subspecies as it was eating a dead kangaroo rat (*Dipodomys*) on the road at 7:30 P.M., May 23, 1946. This was five miles east of Indio, Riverside County, California. The snake was 584 mm. long; the rat was an adult, fairly stiff, and a traffic casualty, as evidenced by a cut on the side.

Birds are occasionally eaten; a sidewinder 530 mm. in length was found to contain a California yellow warbler (*Dendroica aestiva brewsteri*). Another had eaten what appeared to be a desert sparrow (*Amphispiza bilineata deserticola*). Captive specimens eat mice, although they do not feed as readily in captivity as most other species of rattlesnakes. Bogert (1941b, p. 338) fed one a northern crested lizard (*Dipsosaurus d. dorsalis*); he also informed me of another captive that ate a Texas horned toad (*Phrynosoma cornutum*) without apparent ill-effect.

One juvenile, only 292 mm. long, from Wellton Mesa, Yuma County, Arizona, contained a fringe-toed sand lizard (*Uma n. notata*) and a caterpillar. Whether the lizard had eaten the caterpillar first, or was eating it when struck by the snake, could not be determined. One specimen 543 mm. long had eaten both a whiptail lizard and a mouse. Gravel or sand are not infrequently found in the intestinal tracts of sidewinders, no doubt ingested with the prey. Such insect remains as are found were probably contained originally in the stomachs of the lizards.

*Central American Rattlesnake* (*C. d. durissus*).—I have little pertinent information on the feeding habits of this rattler. Twelve specimens that I examined contained mammal hair; another contained feathers, quills, and a kernel of corn. From its large size, this rattler may be presumed to feed principally on mammals, but Picado (1931, p. 49) stated that the spiny-tailed iguana (*Ctenosaura completa*) was a regular prey in one area. March (1928, p. 55) studied it in captivity. He reported (p. 59) that adults would eat rats, guinea pigs, birds, and small iguanas. The young ate lizards (*Cnemidophorus*); he thought in the wild they might be dependent on grasshoppers and other insects.

*Northwestern Neotropical Rattlesnake* (*C. d. culminatus*).—Eight specimens contained mammal hair.

*South American Rattlesnake* (*C. d. terrificus*).—Nine specimens contained mammal hair. Anon. (1894, p. 124) says the Brazilian snakes eat the cony called praia.

*Totonacan Rattlesnake* (*C. d. totonacus*).—Three had mammal hair, and one bird feathers.

*Yucatan Neotropical Rattlesnake* (*C. d. tzabcan*).—Thirteen specimens contained rodent remains.

*Lower California Rattlesnake* (*C. e. enyo*).—This moderate-sized subspecies occurs in the central and southern sections of the peninsula of Baja California, Mexico. Mammal hair, probably from mice, was found in four specimens.

*Timber Rattlesnake* (*C. h. horridus*).—This large rattlesnake of the eastern United States, while primarily preying on small mammals, does eat food of other kinds, probably with greater frequency than most species. Summaries of the range of the timber rattler's prey are thus given by some of my correspondents:

The contents of the majority of the rattlesnakes' stomachs I examined were rabbits, gray squirrels, chipmunks, mountain mice, and grouse eggs. *W. W. Britton, Chambersburg, Pa.*



On several occasions I have noted rattlers that had caught and swallowed adult cottontail rabbits, as well as adult gray squirrels. Small rodents, such as chipmunks, mice, etc., form a large percentage of the diet of the rattlers here in North Carolina. *John H. Stanley, U. S. Forest Service, Andrews, N. C.*

The timber rattlesnakes, *C. h. horridus*, that I have opened have contained small rabbits, rats, mice, moles, frogs, toads, young grouse, or other birds. On one or two occasions I have found a squirrel or chipmunk. *L. E. Close, State Fish Warden, Emporium, Pa.*



I have killed timber rattlesnakes with half-grown rabbits in them, gray squirrels, weasels, rats, toads, birds, garter snakes, grouse, and chickens. *J. W. Crigger, U. S. Forest Service, Huntersville, W. Va.*

Surface (1906, p. 196) found that, of the Pennsylvania snakes he dissected, the food comprised 94 per cent mammals and 6 per cent snakes. However, Surface's results evidently were premised on an examination of only 17 rattlesnakes, one of which had eaten another snake. Uhler, Cottam, and Clarke (1937, p. 608) made much more extensive studies of the timber rattlesnake in the George Washington National Forest in Virginia. They had 253 specimens, of which 141 contained recognizable food items. Mammals comprised 86.9 per cent of the food by volume, birds and their eggs making up the balance, except for a trace of amphibian remains. By number of occurrences, the distribution in per cent was as follows: Mammals, 86.2; birds, 12.6; and amphibians, 1.2.

Surface (1906, p. 196, fig. 23) lists the following mammals disclosed as prey by his studies: six field mice (*Microtus pennsylvanicus*), one jumping mouse (*Zapus hudsonicus*), one white-footed mouse (*Peromyscus leucopus*), one undetermined shrew, one Norway rat (*Rattus r. norvegicus*), one small red squirrel (probably *Sciurus h. hudsonicus*), one rabbit, one common shrew, and three unidentified mammals.

Uhler, Cottam, and Clarke summarize the mammal prey they found as follows, the first figure in each instance indicating the percentage of the total volume of food, the second the number of occurrences: Shrews, 4.86—10; chipmunks and squirrels, 24.79—43; mice, 37.86—65; rabbits, 17.82—23; and other mammals, 1.54—3. Of the mice, white-footed mice (*Peromyscus*) were much the most plentiful, occurring in 47 stomachs. Other mice identified were field mice (*Microtus*) a pine mouse (*Pitymys pinetorum*), a red-backed mouse (*Evotomys carolinensis*), and a jumping mouse (*Napaeozapus insignis*). There was one Norway rat.

Next to the mice, chipmunks (*Tamias striatus*) were most plentiful, being found in 36 stomachs. There were also gray squirrels (*Sciurus carolinensis*) in four, flying squirrels (*Glaucomys*) in three, and the remains of other unidentified squirrels in three. Cottontail rabbits (*Sylvilagus*) occurred in 23 specimens and ranged from juveniles to individuals three-fourths grown. Shrews (*Sorex personatus*, *Blarina brevicauda*, and *Cryptotis parva*) were found in 10 stomachs. One individual contained a bat, and two others unidentified mammals.

Some other published records and lists of mammals are as follows: Dudley (1723, p. 294)—striped squirrels; Kalm (1752—53, p. 59)—hares and minks; Audubon and Bachman (1854, vol. 1, p. 60)—Florida wood rat (*Neotoma floridana*); Metcalfe (1907, p. 124)—chipmunk and small rabbit; Netting (1927, p. 26; 1932, p. 13)—jumping, meadow, and white-footed mice, common rats, shrews, young red squirrels, and young cottontails; Babcock (1929a, p. 14)—short-tailed shrew (*Blarina*) and meadow mouse (*Microtus*); Hubbard (1936, p. 281)—gray squirrels, two-thirds and full-grown; Greenfield (1938, p. 254)—woodland jumping mouse (*Napaeozapus*

*insignis*); King (1939, p. 578)—eastern chipmunks, red and gray squirrels, and cottontails; and Davis and Brimley (1944, p. 11)—rats, mice, rabbits, and squirrels.

Smyth (1949, p. 78) reported the following as prey of the timber rattlesnake in Virginia: Chipmunk (*Tamias striatus fisheri*), shrew (*Sorex c. cinereus*), white-footed mice (*Peromyscus leucopus novaboracensis* and *P. maniculatus nubiterrae*), red-backed mouse (*Clethrionomys gapperi maurus*), woodland jumping mouse (*Napaeozapus insignis*), bog lemming (*Synaptomys cooperi stonei*), and Allegheny wood rat (*Neotoma magister*). One specimen contained three genera—a lemming, a long-tailed shrew, and a white-footed mouse. Barbour (1950, p. 106), in eight timber rattlers from Kentucky, found the chipmunk (*T. s. striatus*), red-backed mouse (*C. g. maurus*), white-footed mouse (*P. m. nubiterrae*), and the jumping mouse (*N. i. roanensis*). The jumping mice predominated—seven, to three chipmunks, and one each of the others. There was also a snail that may have come from the cheek pouch of a chipmunk. Russ (1950, p. 47) reported that the stomachs of a large number of rattlers killed in Elk County, Pennsylvania, contained young rabbits, rats, mice, a black squirrel, and songbirds. A recent newspaper report from Millersburg, Pennsylvania, concerns one rattler that ate a young skunk, and another a mink. Sphar (1953, p. 37) also reported finding a 42-inch *horridus* that had swallowed a mink; this was in Centre County, Pennsylvania. Grizzell (1955, p. 277) reported a rattler that had eaten a young woodchuck (*Marmota monax monax*). This happened in western Maryland.

The following are some mammal-prey reports from my own correspondents:

Gray squirrels, ground squirrels, and frogs have been seen in rattlers which have been killed.  
E. A. Schilling, U. S. Forest Service, Franklin, N. C.



A small rattlesnake, approximately one foot in length, which I collected near Laurel Falls, Great Smoky Mountains National Park, was found to have a white-footed mouse (*Peromyscus*) in its stomach. Another, from Sugarlands Ridge, was 46 inches in length and weighed three pounds five ounces. Upon examining its stomach I found a partly digested, full-grown cottontail rabbit. Arthur Stupka, National Park Service, Gatlinburg, Tenn.

There is no doubt that the timber rattlesnakes eat some birds, including game birds and domestic poultry, but it is to be questioned whether their inroads are particularly serious, in view of their known preferences for small mammals. Probably their occasional visits to the hen house start as expeditions against the rats and mice so often found there. Uhler, Cottam, and Clarke (1939, p. 610) found the remains of game birds in two out of 141 rattlesnake stomachs; one contained the leg of a ruffed grouse, the other what apparently were bobwhite feathers. There were bird remains (other than those of game birds) in 18 stomachs; the species included the yellow-billed cuckoo, brown thrasher, wood thrush, cedar waxwing, blackthroated blue warbler, ovenbird, towhee, grasshopper sparrow, and the remains of other unidentified sparrows and warblers. Nauman (1929, p. 331) found a rattler of this subspecies that had eaten an adult field sparrow and a nestful of nearly grown birds.

As to poultry, as long ago as 1675, Josselyn (p. 26) reported that a rattler had swallowed a live chicken; and B. J. (1765, p. 513) states that one ate a brood of 15 turkeys. Rutledge (1936, p. 148) found a young wild turkey in a specimen he killed, and Erickson (1950, p. 43) also reports that a young turkey was eaten by a

timber rattler. The Millersburg, Pennsylvania, *Sentinel* of September 25, 1953, contained an account of one of these rattlers that contained six wild-turkey eggs; another had eaten a grouse weighing about half a pound.

The following are some of the reports I have received concerning raids by the timber rattler on poultry yards:

I have examined the stomachs of two rattlers that had eaten grown gray squirrels, and one that had two young rabbits in it. And on another occasion I killed a large one near my barn that had a frying-size chicken almost swallowed. *W. A. Spiller, District Warden, Haleyville, Ala.*



I have known timber rattlers to eat chickens, large and small. *H. R. Wright, Waldron, Ark.*



I have seen rattlers kill and try to swallow half-grown chickens. *James T. Hoover, U. S. Forest Service, Plainview, Ark.*

Blakey (1937, p. 13) found a timber rattler that had swallowed four wild-turkey eggs. This was in the Missouri Ozark Range. Fragmentary reports indicate that *horridus* occasionally eats snakes, lizards, and frogs, but I have no corroborative details, beyond the traces of amphibian remains mentioned by Uhler, Cottam, and Clarke (1939, p. 608). Frogs, small fishes, and small snakes are mentioned by Shorey (1953, p. 25).

*Canebrake Rattlesnake* (*C. h. atricaudatus*).—This rattlesnake—one of the largest—is capable, even when young, of eating full-grown mice. It has been known to eat rabbits, tree squirrels, rats, and mice. Birds are sometimes taken.

Some of the reports received from my correspondents are the following:

Our rattlesnakes eat small rabbits, tree squirrels, rats, and birds of all kinds. A six-footer I cut open had two grown squirrels in its stomach. *J. M. Shevlin, Alexandria, La.*



In Louisiana, we found numerous rattlesnakes throughout the north-central portion of the state. On one occasion we discovered one about four feet long that had just eaten two young rabbits that were clearly visible as bumps in its stomach. This individual was very listless and could barely coil to strike. I have also found field mice in others that I killed and dissected. *Ralph C. Bryant, U. S. Forest Service, Ouray, Colo.*



Swamp rattlers [*atricaudatus* ?] prefer rabbits to other animals for food, but will eat squirrels. They will eat small chickens and birds. As you may know, rabbits are cyclic as also are squirrels. I have seen a definite increase in the number of rattlesnakes when there was an abundance of rabbits. *Joseph T. McCullough, U. S. Forest Service, Brooklyn, Miss.*

Goodrum (1940, p. 24) mentions three occasions when rattlesnakes of this subspecies were observed to be eating gray squirrels (*Sciurus c. carolinensis*). Zipperer (1947, p. 30) found one less than five feet long that contained a full-grown squirrel; he was surprised so large an animal could have been swallowed by a snake this size. His investigations showed other food items of this subspecies to be rabbits, rats, birds, and frogs. Clark (1949, p. 260), in the hill parishes of Louisiana, found the following in the stomachs of 30 canebrakes (*atricaudatus*): 10 rabbits, 8 mice, 6 rats, and 1 squirrel. There were also five bobwhites. Keep (1882, p. 27) shot a large rattler in Louisiana that contained several quail. However, Lay (1940, p. 35) apparently does not consider rattlesnakes to be important quail predators, since he fails to mention them in a discussion of animals that make serious inroads on

quail. *Texas Game and Fish* (December, 1953, vol. 12, no. 1, p. 52) contained an illustration of what appears to be a full-grown cottontail rabbit that had been swallowed by a large canebrake rattler. This was near Bellville, Texas.

Allen and Neill (1950c, p. 19) give the following as the food of the canebrake rattler in Florida: Juveniles—mice, young rats, lizards, and small birds; adults (40 examined)—wood rats, barn rats, cotton rats, white-footed mice, pocket gophers, and field sparrows. Occasionally they eat a squirrel or a young rabbit. Some of my correspondents have listed frogs and toads among the food items taken by the canebrake rattler.

*Totalcan Small-Headed Rattlesnake* (*C. i. intermedius*).—Two specimens contained lizards, quite large for so small a snake, and another had lizard scales.

*Omilteman Small-Headed Rattlesnake* (*C. i. omiltemanus*).—One specimen contained a lizard, and eleven had lizard scales and other remains. One had an insect pupal case, which may have come in via a lizard. It is evident that these small rattlers, with their conspicuously small heads, are largely dependent on lizards for food. R. W. Axtell informed me that one lizard preyed on by this rattler is *Sceloporus mucronatus omiltemanus*.

*Mottled Rock Rattlesnake* (*C. l. lepidus*).—Marr (1944, p. 488) found a red scaly lizard (*Sceloporus poinsetti*) in one of these little rattlers. Probably the young are largely lizard feeders; although the adults eat both mammals and lizards, the latter seem to be preferred. Of those that I have examined, seven contained lizard remains as compared with one that had eaten a mammal and one a bird. Milstead, Mecham, and McClintock (1950, p. 557) found that the following had been eaten by specimens collected in Terrell County, Texas: eastern spotted race runner (*Cnemidophorus g. gularis*), Texas tree uto (*Urosaurus o. ornatus*), Texas horned toad (*Phrynosoma cornutum*), a western hook-nosed snake (*Gyalopion canum*), and a frog (*Syrhophus marnocki*). A captive specimen ate several southern ground snakes (*Haldea striatula*). Falck (1940, p. 135) has also reported on its feeding habits in captivity. He fed it mice of various kinds, a number of frogs, and three tiger salamanders. It killed, but refused to eat, a newt (*Triturus viridescens symmetrica*).

*Banded Rock Rattlesnake* (*C. l. klauberi*).—This snake is primarily a lizard eater, even as an adult. I found several with Yarrow's scaly lizards (*Sceloporus j. jarrovi*) and other unidentifiable lizard remains in the intestinal tract. Campbell (1934, p. 10) found two *jarrovi* in one specimen and one in another. Woodin (1953, p. 294) reports having found a mouse and a spiny lizard (probably *Sceloporus clarki*) in Huachuca Mountain specimens. Kauffeld (1943a, p. 350; 1943b, p. 609) has reported on their food habits in captivity. Both adults and young accepted lizards and mice of appropriate sizes. Woodin stated that in captivity *klauberi* preferred dead *jarrovi* to live ones. One specimen of the Tamaulipan rock rattlesnake (*C. l. morulus*) contained lizard scales.

*San Lucan Speckled Rattlesnake* (*C. m. mitchelli*).—The food of this subspecies is no doubt the same as that of its close relatives in California and Arizona. One adult contained mammal hair; another a whiptail lizard (*Cnemidophorus maximus*).

*El Muerto Island Speckled Rattlesnake* (*C. m. muertensis*).—As previously reported (Klauber, 1949b, p. 103), this stunted island subspecies eats lizards and mice. Lizard remains were found in four specimens, and mammals in seven. The lizards were either side-blotch lizards (*Uta stansburiana*) or banded rock lizards (*Streptosaurus mearnsi*); and at least some of the mammals were white-footed mice (*Peromyscus*).

*Southwestern Speckled Rattlesnake* (*C. m. pyrrhus*).—This moderate-sized rattler lives primarily on mammals. Birds are occasionally eaten, and lizards also, the latter especially by the young. Among specimens examined, 18 contained mammal remains, 9 had lizards, and 1 a bird. One had eaten both a mouse and a lizard, another contained lizard and insect residue, but the lizard no doubt accounted for the insects.

Camp (1916, p. 534) reported a speckled rattler in the Turtle Mountains, San Bernardino County, California, that had eaten a Stephens canyon mouse (*Peromyscus crinitus stephensi*). Johnson, Bryant, and Miller (1948, p. 275) observed specimens that had eaten an antelope ground squirrel (*Citellus* [= *Ammospermophilus*] *l. leucurus*) and a white-footed mouse (*Peromyscus truei*). I found a young specimen in Highland Valley, San Diego County, that had swallowed a Gambel white-footed mouse (*Peromyscus maniculatus gambeli*). Other specimens contained the following prey: Dulzura kangaroo rat (*Dipodomys agilis simulans*), southern California side-blotch lizard (*Uta stansburiana hesperis*), spiny lizard (*Sceloporus*), western skink (*Eumeces skiltonianus*), and chuckwalla (*Sauromalus o. obesus*).

Charles Shaw reported a large specimen that contained a nearly grown cotton-tail (*Sylvilagus auduboni sanctidiegi*). Wade Fox told me of finding a speckled rattler in the Joshua Tree National Monument in California about to eat a white-footed mouse caught in a trap. One was observed to eat a dead ground squirrel shot some three hours before. Dean E. Batchelder found one of these rattlesnakes that had eaten eight birds, probably goldfinches. These had been attracted by a small fountain installed as a bird bath at a desert camp. Evidently the snake had lain in wait for prey at this fruitful spot.

Another report is the following:

While I was fishing in a stream on the westerly slope of the San Pedro Mártir Mountains of Lower California, I heard a rattler a few feet ahead in a thicket of willows. I located it with some difficulty and observed that it had the head of a full-sized ground squirrel in its mouth. I threw a large rock at the snake, injuring it slightly, whereupon it disgorged the squirrel, which was already dead. The snake proved to be a speckled rattler (*C. m. pyrrhus*). Allan S. Klauber, San Diego, Calif.

*Panamint Rattlesnake* (*C. m. stephensi*).—This subspecies is known to feed on small mammals and lizards. Merriam (in Stejneger, 1893, p. 215) found a specimen that had eaten a kangaroo rat (*Dipodomys*) and a pocket mouse (*Perognathus*). Russell K. Grater wrote me that he had dissected specimens that had eaten a pocket mouse, an antelope ground squirrel (*Citellus*), and a zebra-tailed lizard (*Callisaurus draconoides gabbi*). I saw one that had eaten a full-grown desert whiptail lizard (*Cnemidophorus t. tigris*).

*Northern Black-Tailed Rattlesnake* (*C. m. molossus*).—I have in my collection a specimen from the Santa Catalina Mountains of Arizona that had eaten a white-

throated wood rat or pack rat (*Neotoma a. albigula*), and Earl Jackson of the National Park Service found a rat of this species in a *molossus* at Montezuma Castle National Monument. Milstead, Mecham, and McClintock (1950, p. 557) report the Encinal mouse (*Peromyscus pectoralis*) as a food item of *molossus* in Terrell County, Texas. Vorhies and Taylor (1940, p. 508) found that large specimens in captivity would eat two or three wood rats at a feeding. Woodin (1953, p. 295) says that captive specimens eat dead mice or kangaroo rats. I found unidentified mammal hair in 11 northern blacktails.

*Mexican Black-Tailed Rattlesnake* (*C. m. nigrescens*).—Mammal remains (one a *Neotoma*) were found in seven specimens, and lizard scales in one.

I have no data on the food of the San Esteban Island blacktail (*C. m. estebanensis*). Both mammals and lizards occur on the island.

*Mexican Lance-Headed Rattlesnake* (*C. polystictus*).—One contained mammal hair; another a small passerine bird and a small rodent.

*Arizona Twin-Spotted Rattlesnake* (*C. p. pricei*).—A specimen from Graham Mountain, Arizona, disgorged an adult field mouse. This snake was about 470 mm. long. I found lizard remains in nine specimens varying in length from 258 to 479 mm. Such remains as could be identified were Yarrow's scaly lizards (*Sceloporus j. jarrovi*). Gloyd (1937, p. 132) also found the scales of this lizard in one specimen. Woodin (1953, p. 295) reported a *pricei* containing a *jarrovi* almost too large for it to engulf. Kauffeld (1943a, p. 353; 1943b, p. 609) has discussed the food habits of captive specimens of *pricei*; he found that they preferred lizards.

I have no data on the food habits of the subspecies *C. p. miquihuanus*.

*Tancitaran Dusky Rattlesnake* (*C. pusillus*).—Two specimens contained lizard scales in the digestive tract. Dr. F. A. Shannon informed me that one lizard eaten by this rattler is *Sceloporus f. ferrari perezi*. One specimen had eaten a spiny pocket rat.

*Red Diamond Rattlesnake* (*C. r. ruber*).—This large rattlesnake, like most of the diamondbacks, generally feeds on mammals, particularly rabbits, ground squirrels, and rats. Of the specimens I examined, 53 contained mammal remains, three had eaten lizards, and one a bird. Large specimens have been known to eat cottontail rabbits (*Sylvilagus auduboni sanctidiegi*), brush rabbits (*Sylvilagus bachmani cinerascens*), and ground squirrels (*Citellus b. beecheyi*). Tevis (1943, p. 242) has given a detailed account of watching a red diamond rattler catch and eat antelope ground squirrels (*Citellus* [= *Ammospermophilus*] *l. leucurus*). This same individual readily seized and ate a kangaroo rat (*Dipodomys*) when it was tossed to it. In a specimen from Jamul, San Diego County, I found a young skunk (*Spilogale gracilis microrhina*). Juveniles are believed to live largely on such mice and rats as *Peromyscus*, *Microtus*, and *Neotoma*, but they occasionally eat lizards. In fact, I have found whiptail lizards (*Cnemidophorus t. multiscutatus*) in subadult red diamond rattlers measuring 886 and 920 mm. in length.

*San Lucan Diamond Rattlesnake* (*C. r. lucasensis*).—This large rattlesnake feeds mostly on mammals. Specimens brought to the San Diego Zoo disgorged cottontail rabbits (*Sylvilagus auduboni confinis*) and black-tailed kangaroo rats (*Dipodomys*

*merriami melanurus*). But *lucasensis* does not scorn lizards, even after it has attained adult size, for one, 1,155 mm. long contained parts of a spiny-tailed iguana (*Ctenosaura hemilopha*). Of a number whose intestinal tracts were examined, 22 contained mammal hair, whereas reptile remains could be recognized in only three.

*Mojave Rattlesnake* (*C. s. scutulatus*).—This desert subspecies is largely a mammal feeder. I found mammal remains in the intestinal tract of 21 specimens and lizard scales in only two. One individual contained insect remains as well as those of a centipede. C. M. Bogert encountered one eating a kangaroo rat (*Dipodomys*) in the Antelope Valley, California, at 10 p.m. L. M. Huey (1942, p. 375) found one in the Organ Pipe Cactus National Monument, southern Arizona, that contained a round-tailed ground squirrel (*Citellus tereticaudus neglectus*). Johnson, Bryant, and Miller (1948, p. 275) found a small *scutulatus* with a half-swallowed adult pocket mouse (*Perognathus longimembris*), and another contained a whiptail lizard (*Cnemidophorus tigris*). Vorhies and Taylor (1940, p. 508) fed captive specimens on white-throated wood rats (*Neotoma a. albigula*). A Mojave rattler, while being carried in a sack by a collector, ate a leaf-nosed snake (*Phyllorhynchus d. perkinsi*).

*Huamantlan Rattlesnake* (*C. s. salvini*).—Mammal remains were found in two specimens of this southern subspecies of *C. scutulatus*.

*Long-Tailed Rattlesnake* (*C. stejnegeri*).—A specimen contained mammal hair.

*Tiger Rattlesnake* (*C. tigris*).—I found mammal hair in the intestinal tract of an adult. Ortenburger and Ortenburger (1926, p. 119) came upon one eating a whiptail lizard (*Cnemidophorus melanostethus*). Kauffeld (1943a, p. 35) found that this species would eat lizards in captivity. This is a rattlesnake remarkable for the small size of its head, so that it may be presumed to feed on lizards to a greater extent than other rattlesnakes of similar body size.

*Tortuga Island Diamond Rattlesnake* (*C. tortugensis*).—This rattlesnake is known to feed on mice. Several of my specimens contained mammal hair. A white-footed mouse, *Peromyscus dickeyi*, is plentiful on Tortuga Island, in the Gulf of California.

*Cross-Banded Mountain Rattlesnake* (*C. transversus*).—One specimen contained lizard scales.

*Central Plateau Dusky Rattlesnake* (*C. t. triseriatus*).—Davis and Smith (1953, p. 142) found a frog in one specimen and a wood rat (*Neotomodon alstoni*) in another. This subspecies seems to divide its diet about equally between mammals and lizards, as I found 13 specimens to contain mammal hair, and the same number with lizard remains. One of the lizards was a skink. A salamander was found in a young specimen only 193 mm. long. Large and well-preserved insect remains were found in such numbers as to suggest that they may have been eaten directly by the rattlers, rather than having been brought in as the stomach contents of lizards. These included a beetle elytron, remains of a cricket (Gryllidae) and a Jerusalem cricket; also the jaws and head of a centipede.

*Queretaran Dusky Rattlesnake* (*C. t. aquilus*).—In this subspecies, specimens containing lizard remains outnumbered those with mammal hair 19 to 2. Several of

the lizards were spiny lizards (*Sceloporus*); one was a gecko, and one a gerrhonotid. There were also a frog, a cricket, and a spider (Argiopidae).

*Aruba Island Rattlesnake* (*C. unicolor*).—This species is said to prefer rabbits and lizards. In captivity it readily eats mice.

*Prairie Rattlesnake* (*C. v. viridis*).—This rattlesnake, which grows to a large size—up to four feet or more, in some areas—depends principally on mammals for its food supply, but also preys to some extent on birds and their eggs, lizards, frogs, and possibly insects.

The following are some of the reports on the feeding habits of this rattler sent me by correspondents:

I have seen prairie rattlesnakes in the process of swallowing the young of the cottontail rabbit, gophers, and small birds; and I have opened them and found ground squirrels and mice in the digestive organs. *Glenn Flathers, U. S. Forest Service, Camp Crook, S. Dak.*



I have observed prairie rattlesnakes for about 20 years and have found that they prey on young rabbits, ground squirrels, prairie dogs, mice, and birds. *W. J. Petermann, U. S. Forest Service, Meeteetse, Wyo.*



I have heard it said that rattlesnakes, prairie dogs, and owls live peacefully together in the same holes, but I don't believe it. Once I found a rattlesnake swallowing a prairie dog somewhat over half-grown. *Roy C. Spangler, Predatory Animal Hunter, La Veta, Colo.*



I found a large rattler near Paradise, Montana, that had just devoured a full-grown Columbian ground squirrel. He was approximately three feet long, and was awkward and sluggish because of the big load he was carrying in his stomach. *C. K. Lyman, Newport, Wash.*



Once, during the summer of 1934, while at Fort Niobrara National Wildlife Refuge, Nebraska, I set a large spring trap under my cabin to catch what I thought was a skunk. I was awakened at about 10 P.M. by a furious threshing and buzzing, and found a large female prairie rattlesnake caught in the trap. She had eaten a nearly full-grown cottontail rabbit. When crawling under the cabin, the rabbit had sagged, springing the trap. *W. E. Beed, Fish and Wildlife Service, Waupun, Wis.*



I have examined the stomach contents of prairie rattlers and have never found anything but gophers.<sup>3</sup> Possibly 50 stomachs were examined over a period of years. *William Lakanen, Game Warden, Rawlins, Wyo.*

Coues and Yarrow (1878, p. 268) mention the prairie squirrel (*Spermophilus* [*Citellus*] *richardsoni*) as being among the prairie rattler's prey. Williston (1878, p. 209) and Brons (1882, p. 565) report that these rattlers feed extensively on young prairie dogs (*Cynomys l. ludovicianus*).

These accounts stress the larger rodents as comprising the prey of the prairie rattler. Without doubt they also feed to an important extent on the smaller creatures of the plains, grouped under the terms rats and mice, especially kangaroo rats (*Dipodomys*), wood rats (*Neotoma*), pocket mice (*Perognathus*), harvest mice (*Reithrodontomys*), white-footed or deer mice (*Peromyscus*), and meadow mice (*Microtus*). Marr (1944, p. 488) mentions one that had fed on an upland meadow mouse (*M. haydeni*). Bateman (1918, p. 501) examined the stomachs of 158 prairie

<sup>3</sup> No doubt small ground squirrels (*Citellus*), which are generally called gophers in the prairie states.

rattlers in connection with a prairie-dog control project. Of those containing food, about half had eaten meadow mice (*Microtus*), and about half lark buntings (*Calamospiza*). Hamilton (1950, p. 34) found *Microtus* in each of seven specimens collected in southwestern South Dakota. Mosimann and Rabb (1952, p. 26) observed that *viridis* in Montana had eaten deer mice (*Peromyscus maniculatus artemisiae*). As rodent destroyers these snakes have great economic merit; it is unfortunate that this valuable quality should be counterbalanced by the danger of snake bite to human beings and stock.

A. M. Jackley, at that time South Dakota rattlesnake control officer, had this to say about the frequency with which birds are eaten by prairie rattlers:

I frequently find that rattlers have fed on mature birds up to the size of meadow larks. I captured a dozen rattlers within a mile of a den last spring that had gotten their first meal. Eight had caught birds and four had eaten rodents. Among the birds there were four meadow larks, a towhee, a catbird, and two horned larks. The rodents were 13-striped gophers<sup>4</sup> and one mole. I hunted along the Bad River early in June where there are ring-necked pheasants, and found two rattlers that had taken young pheasants, three with young grouse, and nine that had eaten rodents.

Other reports of correspondents who found evidence that prairie rattlers prey on birds follow:

Once I saw a rattlesnake robbing a meadow lark's nest. When I first saw the snake it had part of the last small bird still sticking out of its mouth. I killed the snake with a shovel and cut him open in several places, but found nothing except four small birds. The birds were not feathered out yet. *Eddie Buchta, U. S. Fish and Wildlife Service, Moneta, Wyo.*



I killed a rattlesnake and opened him up and found six young meadow larks in his stomach. These birds were nearly old enough to fly. And once I found in a rattler a young rabbit that I would say must have been six weeks old. The rattler was three and a half feet long. *Judge W. S. Owens, Cody, Wyo.*



I have killed a good many rattlers in this vicinity but only investigated the stomach contents of two. One snake contained five fully feathered meadow larks; the other, a large rat or small prairie dog. *Howard L. Munson, U. S. Fish and Wildlife Service, Newcastle, Wyo.*

Other records of birds eaten by prairie rattlers, as mentioned in letters I have received, included robins and a raven. Austen S. Cargill informed me that once when hunting grouse in South Dakota, he brought down two birds. After retrieving the first, he sought out the second and found that it was being swallowed by a prairie rattler. Williston (1878, p. 203) found that these rattlesnakes had eaten slum larks and lark finches (*Chondestes grammaca*). Brons (1882, p. 585) said that they ate the young and eggs of the burrowing owls (*Speotyto cunicularia hypogaea*), with which they are so often presumed to live in peaceful tenancy in the prairie-dog towns.

Other reports of egg-eating are these:

For years I have made it a practice to open rattlesnakes I have killed to investigate suspicious bulges. On several occasions I have found frogs which had been swallowed head first; also, young horned larks and other unidentified young birds. A particularly heavy-set fellow I killed one morning in my hen house had an unbroken egg about midway down. *F. R. Cochran, U. S. Forest Service, Sundance, Wyo.*

<sup>4</sup> *Citellus tridecemlineatus*.

I lived in northeastern Colorado for 25 years, and found lots of rattlers. I have seen them eat eggs where the birds nested on the ground. *Charles G. Holzworth, Game Warden, Kremmling, Colo.*

C. B. Perkins, who collected prairie rattlesnakes at denning time near Platteville, Colorado, found that young of the year regurgitated lizards, including northern earless lizards (*Holbrookia m. maculata*) and northern prairie swifts (*Sceloporus undulatus garmani*). Larger specimens usually disgorged mice, thought to be *Peromyscus*. Mr. Perkins was told of a large specimen that had swallowed an eastern short-horned horned toad<sup>3</sup> (*Phrynosoma douglassi brevirostre*). Hamilton (1950, p. 34) found two prairie rattlers that had eaten horned toads of this subspecies.

Several correspondents state that the prairie rattlesnake eats toads and frogs, but no details are given. I judge, from observations of related subspecies, that they probably eat frogs occasionally. C. H. McDonald, U. S. Forest Service, Stevensville, Montana, wrote that he had force-fed a large rattler with a big toad, but it was thrown up several days later. Stabler (1948, p. 168) found a *viridis* near Colorado Springs that had eaten a spadefoot toad. Several correspondents mention such insects as grasshoppers and Mormon crickets as having been eaten by this rattler. Sometimes arthropods such as these are ingested with prey, and their remains outlast the creatures that originally ate them. I have little doubt that such insects are occasionally eaten but lack definite proof.

*Grand Canyon Rattlesnake* (C. v. *abyssus*).—One specimen contained a lizard of the genus *Sceloporus*; another, mammal hair.

*Coronado Island Rattlesnake* (C. v. *caliginis*).—This subspecies differs from the mainland *helleri* in that it feeds primarily on lizards, and this in spite of the fact that South Coronado Island is well populated with rodents that an adult *caliginis* could cope with quite successfully. I am told by L. M. Huey that the Coronado Island white-footed mouse (*Peromyscus maniculatus assimilis*) is relatively abundant on the island. C. v. *helleri*, on the mainland, feeds primarily on mammals, although lizards comprise an important part of the diet of the juveniles. But *caliginis* does not modify its propensity for lizards even when it has reached a size such that it could eat mice. Of the 20 specimens examined that contained recognizable food remains, only one had mammal hair, and this is the more remarkable since hair is recognizable until the feces are voided, which is not always true of lizard scales. The other 19 contained lizard remains; six could be recognized as alligator lizards (*Elgaria multicarinata nana*), three as skinks (*Eumeces skiltonianus*), and one as a side-blotch lizard (*Uta stansburiana hesperis*). The other nine were too completely digested to be identified. A large alligator lizard is a full meal for an adult *caliginis* (Klauber, 1949b, p. 95). Zweifel (1952, p. 10) reported that, of eight specimens of *caliginis* examined, two had eaten skinks while four contained alligator lizards.

*Arizona Black Rattlesnake* (C. v. *cerberus*).—Two specimens were found to contain mammal remains. One of the paratypes was reported to have eaten a bluebird (*Sialia mexicana*). I have received reports that this subspecies has been found to

<sup>3</sup> Actually a lizard (*Phrynosoma*), not a true toad.

have eaten western mockingbirds (*Mimus polyglottos leucopterus*) and Arizona warblers (*Dendroica*). It should not be thought from these few records that *cerberus* preys to a greater extent on birds than does *oreganus* or *helleri*. Probably, were adequate data available, it would be found that mammals constitute a major part of the food of the adults, and lizards a moderate part of the diet of the young.

*Midget Faded Rattlesnake* (C. v. *decolor*).—Three specimens that I examined contained mammal remains. Undoubtedly this subspecies is also a lizard feeder, if we may judge from its close relatives (particularly *lutosus*) and the facts that it is both small in size and inhabits an area with a plentiful lizard population.

*Southern Pacific Rattlesnake* (C. v. *helleri*).—This moderately large rattlesnake, like the other *viridis* subspecies, subsists primarily on mammals, although the young depend somewhat on lizards. Birds are occasionally eaten. In my own investigations of the stomach contents of southern Pacific rattlers I found that among small and medium-sized snakes—those not exceeding 650 mm. in length over-all—there were 134 with mammal hair in the intestinal tract compared with 26 with lizard scales and one with bird feathers. However, I feel that this is not an unbiased feeding record of the juvenile and adolescent snakes, for mammal hair is always easily recognizable as long as it remains in the digestive tract, while lizard scales can sometimes be found only after a most careful investigation, and may, in some species, be so completely disintegrated as to be unidentifiable. Such mammals as could be identified in these specimens were mostly pocket mice (*Perognathus*), white-footed mice (*Peromyscus*), or meadow mice (*Microtus*). Two were an adult female Gambel white-footed mouse (*Peromyscus maniculatus gambeli*) in a southern Pacific rattler from Poway, San Diego County, and an adult San Diegan short-eared pocket mouse (*Perognathus f. fallax*) in a specimen from Lyons Valley, San Diego County. Two baby rattlers only 300 mm. long had each eaten two mice of undetermined species, and another had eaten a mouse and a lizard.

Among the food notes in this subspecies supplied by my correspondents are the following:

I found a southern Pacific rattler swallowing a brush rabbit\* at 11 A.M., May 8, 1938. When the rattler saw me it backed up, dragging the rabbit, and then regurgitated it. The snake was 29 inches long. *A. C. Wallen, Los Angeles, Calif.*



In Mission Gorge I came upon a southern Pacific rattlesnake swallowing a third-grown San Diegan cottontail rabbit (*Sylvilagus auduboni sanctidiegi*). It was being eaten head first, and the front feet, which were compressed against the sides, were still showing, although the shoulders were within the snake's mouth. Another time, on North Cuyamaca Peak, I found one that had swallowed a half-grown ground squirrel (*Citellus beecheyi nudipes*). This meal had not been digested and the snake lay torpid in the shade beneath a bush. *L. M. Huey, San Diego Society of Natural History, San Diego, Calif.*

Mr. Huey also told me of a nimble kangaroo rat (*Dipodomys agilis cabazonae*) that had been eaten by a rattler of this subspecies. Notes from two other correspondents follow:

I have cut two rattlers open that had recently fed. The first was in the sand dunes in the extreme southwestern corner of San Luis Obispo County. This snake had swallowed a half-

\* Ashy brush rabbit (*Sylvilagus bachmani cinerascens*).

grown brush rabbit.<sup>7</sup> The other had swallowed a half-grown digger squirrel. This was on the Klamath River about half-way between Hornbrook and Copco.<sup>8</sup> *Louis Olive, Alturas, Calif.*



I found a southern Pacific rattler eating a trade rat (*Neotoma albigula*) on the desert slope of Hot Springs Mountain, in eastern San Diego County. *Edmund C. Jaeger, Riverside, Calif.*

Most of my correspondents agree that the principal large mammals eaten by this rattler are young cottontail or brush rabbits, and ground squirrels. The following are the rattler's mammal food items identified in published articles: Grinnell and Grinnell (1907, p. 53; Grinnell, 1908, p. 169)—Fisher ground squirrel (*Citellus beecheyi fisheri*), San Bernardino chipmunk (*Eutamias speciosus*), Merriam chipmunk (*Eutamias merriami*), meadow mouse (*Microtus californicus*), and San Bernardino mountain pocket gopher (*Thomomys altivallis*); Atsatt (1913, p. 44)—half-grown ground squirrels and adult wood rats (*Neotoma*).

Ornithological prey are mentioned in the following:

On a little-used truck trail between Tanbark Flats and Sunset Peak Lookout in the Angeles National Forest, Los Angeles County, we saw a southern Pacific rattlesnake crossing the road just in front of the car and ran over it. We found that it had eaten a roadrunner (*Geococcyx californicus*). It was an odd incident, for these birds are supposed to kill rattlers. *Glen E. Sindel, U. S. Forest Service, Descanso, Calif.*

Several correspondents mention the California or valley quail (*Lophortyx californicus*) as prey of the southern Pacific rattlesnake, and two include the mourning dove (*Zenaidura macroura*) among the birds eaten. Pierce (1933, p. 62) came upon a *helleri* in the San Bernardino Mountains while it was eating a third-grown plumed or mountain quail (*Ortyx picta plumifera*). The snake was less than three feet long.

Chickens and turkeys are sometimes taken.

I can state positively that rattlesnakes, besides eating ground squirrels and small rabbits, take birds, including doves, small chickens, and turkeys, for I have seen them prey on all of these. They took small chickens and turkeys from my coops. The coops were small ones in which we kept one turkey, or one chicken, and her brood. The snakes only took very young ones—say up to three weeks old. *M. W. Durham, U. S. Forest Service, Pasadena, Calif.*

Southern Pacific rattlesnakes, like many other kinds, particularly in the southwest, feed on lizards to some extent. This is especially true of the young, which can more easily swallow a lizard, with its attenuated body, than a thicker-set mammal. Among the lizards that I have found in the stomachs of these rattlers are the western fence lizard (*Sceloporus occidentalis biserialatus*), granite spiny lizard (*Sceloporus o. orcutti*), southern mountain swift (*Sceloporus graciosus vandenburgianus*), southern California side-blotch lizard (*Uta stansburiana hesperis*), western skink (*Eumeces skiltonianus*), coastal whiptail (*Cnemidophorus tigris multiscutatus*), and the San Diegan alligator lizard (*Elgaria multicarinata webbi*). One rattler may have eaten a tubercular gecko, but the condition of the specimen made the identification doubtful.

Southern Pacific rattlers rarely eat amphibians. Von Blocker (1942, p. 38) reported the remains of a toad in one specimen; besides this, it contained three Jerusalem crickets and four mammals, and was trying to swallow another, a rather incredible repast.

<sup>7</sup> Ashy brush rabbit (*Sylvilagus bachmani cinerascens*).

<sup>8</sup> The second record refers to *C. v. oregonus*.

*Great Basin Rattlesnake* (*C. v. lutosus*).—The Great Basin rattlesnake, like the others to which it bears a subspecific relationship, is a snake of moderate size that feeds primarily on small mammals, but occasionally on birds, and also on lizards, particularly when young. Lizards are extremely plentiful in some of the areas it inhabits, from which it may be judged that the mammals available for the mature snakes may be a more important limitation on the rattler population than the lizards for the juveniles, as is the case with some subspecies.

My correspondents have listed, as the prey of this rattlesnake, young jackrabbits, cottontails, pine squirrels, chipmunks, gophers, rats, and mice. A few quotations from their letters are these:

I have seen rattlesnakes eating mice and gophers. It takes them several minutes to swallow a large-sized gopher. I have also seen one trying to swallow a fair-sized baby rabbit. *Albert Madarieta, Oakley, Idaho.*



On two occasions I have found rattlesnakes devouring squirrels. One squirrel was a pine squirrel, the other a Columbian ground squirrel. *E. L. Thompson, U. S. Forest Service, Cascade, Idaho.*



A few years ago I killed what I believe to be the longest and heaviest rattlesnake ever taken in Oregon. The location was at the diversion dam where the Blitzen River emerges from the canyon at French Glen, Harney County. The snake measured 53 inches. It had just swallowed a young jackrabbit which measured 12 inches from nose to the tip of a hind foot. The snake tried to crawl into a loose pile of rocks, but the large lump formed by the recently swallowed rabbit kept him from going in. On other occasions I have found a red-backed mouse (*Evotomys*) and a meadow mouse (*Microtus*) in the stomachs of rattlesnakes. *Stanley G. Jewett, Portland, Oreg.*



A rattler captured east of Bear Lake, Bear Lake County, Idaho, had swallowed a large Columbian ground squirrel. The squirrel was disgorged after the snake was captured. *Earl C. Sanford, U. S. Forest Service, Vernal, Utah.*



I found a Great Basin rattlesnake shortly after it had swallowed a Columbian ground squirrel. The snake was very lazy and all swelled up around the squirrel. It was hard to see how he got it through his jaws. *J. W. Stokes, U. S. Forest Service, Ogden, Utah.*

Benjamin Banta told me of a *lutosus* that had eaten a kangaroo rat (*Dipodomys*). Another known food item is the pocket mouse (*Perognathus parvus*). Ira La Rivers of the University of Nevada writes me that the rattlers of western Nevada often prey on the Piute ground squirrel (*Citellus townsendi mollis*) and white-footed mice of the genus *Peromyscus*. Printed accounts mention the following mammal prey: Piute ground squirrel (*C. t. mollis*)—Richardson (1915, p. 434) and Pack (1930, p. 22); yellow pocket gopher (*Thomomys perpallidus aureus*)—Woodbury (1931, p. 116); antelope ground squirrel (*C. l. leucurus*)—Hall (1946, p. 317); Piute ground squirrel (*C. t. mollis*) and dark kangaroo mouse (*Microdipodops megacephalus paululus*)—Fautin (1946, p. 294).

As to birds, Ira La Rivers (1942, p. 66; 1944, p. 428), discussing the nesting mortality of the Brewer blackbird (*Euphagus cyanocephalus*), states:

Coming home after dark one warm evening, I was playing the flashlight on the ground before me, for the location of a rattlesnake den nearby made some caution necessary. Passing Nest 90, the light centered on a medium-sized rattler lying across one side of a small sagebrush, the branches bending over under his weight. The snake remained motionless

over the nest for a moment, then, as I stood immobile, reached in and took the remaining nestling in his jaws, swallowing the tiny bird with no difficulty. Then he unobtrusively slid from the bush and made off leisurely.

The same author wrote me:

I found, from the contents of a rattler's stomach, that the wary little horned lark (*Otocoris alpestris leucolaema*) is an occasional victim, undoubtedly taken at night while brooding on her nest, which is usually built on the ground beneath rabbit brush and sagebrush.

Another communication illustrating the bird-eating propensity of the Great Basin rattlesnake is as follows:

I noticed a rattler lying in the horse trail about 9:30 A.M. At the same time I saw a little wren on a sage bush, fluttering its wings. All at once the rattler struck for its prey. In less than three minutes it had swallowed this small bird, and lazily crawled into the sagebrush for shade. W. V. Connary, Bancroft, Idaho.

One correspondent includes grouse among the prey of this rattler, while another states that it has been known to swallow a hen's egg.

Woodbury (1933, p. 8) found a Great Basin rattler 29 inches long eating a young, but full-feathered, Woodhouse jay. Another ate a western chipping sparrow. Jewett (1939, p. 30) saw a rattler strike and kill a California quail. Fautin (1946, p. 294) found one specimen that contained a horned lark (*Otocoris alpestris utahensis*) and saw another catch a vesper sparrow (*Pooecetes gramineus confinis*).

In my examinations of the contents of the intestinal tracts of Great Basin rattlers I have found mammal hair more frequently than lizard scales in a ratio of about three to one; the young specimens contained the lizard remains. They were seldom identifiable, but one was a sagebrush swift (*Sceloporus g. graciosus*). Pack (1930, p. 22) mentions two juveniles that had eaten lizards of this species. Benjamin Banta told me of one rattler that had eaten a desert whiptail lizard (*Cnemidophorus t. tigris*). One of my correspondents reported that he saw rattlers gathered around a dead sheep for the purpose, he thought, of catching the flies that swarmed about. It may have been that they were seeking the lizards that find a dead animal a fruitful place at which to seek their insect food.

Two of my correspondents mention toads and frogs as being among the food items consumed by the Great Basin rattler. The fact that they do eat frogs is fully verified by this particularly detailed communication from Ira La Rivers:

During the spring of 1934 (May-June) I opened four *lutosus* whose stomachs contained leopard frog (*Rana pipiens*) remains, and on one occasion I saw a large rattler capture a frog of the same species. The small pond containing the frogs was some 15 feet long and 8 feet wide, and lay at the northern edge of the area covered by the blackbird nesting colony which I previously reported on, and nearly due east of the ridge containing the one and only large rattlesnake den in the vicinity. There were numerous garter snakes about, none very large, which preyed upon the frogs, but this is the only spot I have found where *Crotalus* seemed to hunt frogs persistently. The one direct instance of capture I noted occurred while I was sitting beside the pool on a very dark night with a bull's-eye lantern, trying to catch some frogs. I was considerably startled (to put it mildly) by the scream of a frog about 10 yards away. You're undoubtedly acquainted with the unearthliness of the sound; and although I had heard it a couple of times before, when garter snakes captured frogs, it has never failed to startle me. I flashed the light over and spotted a large rattler holding a medium-sized *pipiens* in his mouth, the frog's head hanging on one side, its legs on the other. At the time I first saw it, the frog gave a couple of spasmodic kicks, then lay still. I presume the snake struck just before the frog's cry; if so, death seemed little short of

instantaneous, although it could have occurred as easily from the mechanical damage of the snake's large fangs to some vital center as from the venom. At any rate, the snake apparently struck and kept his hold—not releasing the victim to die, as seems to be the case generally. As soon as the frog was quiet, the snake easily ingested it, and made off leisurely, after a short rest.

*Arizona Prairie Rattlesnake* (*C. v. nuntius*).—I found mammal hair in five specimens. It is probable that the young feed to a large extent on lizards, particularly the speckled earless lizard (*Holbrookia maculata approximans*) which is very common in many areas inhabited by *nuntius*. The latter, one of the smaller subspecies of the western rattlesnake (*C. viridis*), is probably even more dependent on lizard food, when young, than its larger relatives, which are known to feed on lizards to a considerable extent.

*Northern Pacific Rattlesnake* (*C. v. oreganus*).—Most reports on the food habits of this rattlesnake stress its preference for mammals. However, it is known to eat birds and their eggs, reptiles (lizards are especially suitable food for the young), and amphibians. Among the mammals reported by my correspondents as its prey are young jackrabbits, cottontails, brush rabbits, snowshoe rabbits, gray squirrels, pine squirrels, chipmunks, digger and rock squirrels, ground squirrels, marmots, muskrats, kangaroo rats, wood rats, domestic rats, pocket gophers, voles, pocket mice, meadow mice, white-footed mice, red-backed mice, jumping mice, and house mice.

Some typical summaries that I have received are the following:

The food of the rattlesnakes hereabouts consists of all kinds of mice, small birds, including robins, sometimes, and rabbits, squirrels, and chipmunks. *Marion E. Rose, Pateros, Wash.*



The food of the northern Pacific rattlesnake in this area consists largely of young marmots, pocket gophers, mice, voles, bush rats, squirrels, chipmunks, immature muskrats, among rodents; and Gambel, vesper, and Savannah sparrows, and other small ground-nesting birds. The largest rodent eaten in my experience was a marmot<sup>9</sup> measuring nine inches, exclusive of its tail. The snake, which was 2 feet 10 inches long, was so distended that it resembled an inflated tire, and its scales, instead of lying one over the other, stood out separately, revealing the shiny skin between. Within a few yards was another young marmot still warm, and two more snakes of 2 feet 10 inches, and 3 feet 4 inches, evidently about to dispute possession of their victim. On another occasion, while poised on a log and about to step down, I saw beneath me a large rattler with greatly distended body. With some difficulty I recovered my balance and, having duly dispatched him, found that he had swallowed a half-grown muskrat.<sup>10</sup> Another time I killed a big specimen that was lying on a flat slab of stone underneath which lay two young marmots, cold and stiff, which it had presumably decided were rather beyond its stomachic capacity. *A. C. Mackie, Vernon, B. C.*



The prey I have known rattlesnakes to kill consisted of Columbian ground squirrels, pocket gophers, chipmunks, and mice. *George W. Case, U. S. Forest Service, Saint Maries, Idaho.*



The rattlesnake food consists mainly of rock squirrels, gophers, mice, and newly hatched birds. *Jesse L. Harris, Pilot Rock, Oreg.*



I have examined rattlesnake stomachs and found squirrels, rats, mice, small birds, eggs, and other things that might have been insects, but they were hard to identify. *Clarence R. Ousley, Napa, Calif.*

<sup>9</sup> Pallid yellow-bellied marmot (*Marmota flaviventris avara*).

<sup>10</sup> Rocky Mountain muskrat (*Ondatra zibethica osoyoosensis*).

I have found the stomach contents of rattlers along Cortina Creek to include squirrels, quail, and doves. Rarely there are other small birds. Squirrels predominate, for Cortina Creek is alive with them. *R. M. Williams, Arbuckle, Calif.*



The prey of rattlesnakes in this area consists mostly of squirrels, rats, mice, lizards, and, occasionally, small birds, and chickens. They frequent the places where food is plentiful, such as areas infested by squirrels, wood-rat nests, or buildings where there are mice. *Bernie I. Leas, U. S. Forest Service, Platina, Calif.*

The most complete studies that have been published on the feeding habits of any kind of rattlesnake are those by Fitch and Twining (1946, p. 64) and Fitch (1949a, p. 547) on the northern Pacific rattler, at the San Joaquin Experimental Range, a co-operative range and livestock management project carried on by the United States Forest Service, the University of California, and other agencies in Madera County, California. The ecological conditions on the Range were described by Talbot, Nelson, and Storie (1942, p. 7). The methods used by the snakes in finding their prey, as outlined by Fitch and Twining, are quoted at length elsewhere (pp. 645, 647, 648). The list of the animals eaten is here repeated as table 9:1, with the common names of the prey added:

TABLE 9:1  
FOOD OF THE NORTHERN PACIFIC RATTLESNAKE  
RESEARCHES OF FITCH AND TWINING

Prey items	Stomach examinations		Scatological examinations	
	Number of prey items	Per cent of total	Number of prey items	Per cent of total
Ground squirrel ( <i>Citellus beecheyi</i> ).....	23	26.44	37	41.11
Pocket gopher ( <i>Thomomys bottae</i> ).....	8	9.20	2	2.22
Pocket mouse ( <i>Perognathus</i> ).....	10	11.49	2	2.22
Kangaroo rat ( <i>Dipodomys heermanni</i> ).....	5	5.75	24	26.67
White-footed mouse ( <i>Peromyscus</i> ).....	10	11.49	4	4.44
Wood rat ( <i>Neotoma fuscipes</i> ).....	1	1.15	4	4.44
Meadow mouse ( <i>Microtus californicus</i> ).....	3	3.45	1	1.11
Unidentified mouse.....	0	0.00	2	2.22
Cottontail ( <i>Sylvilagus auduboni</i> ).....	14	16.09	3	3.33
Subtotal mammals.....	74	85.06	79	87.78
California quail ( <i>Lophortyx californica</i> ).....	1	1.15	1	1.11
Brown towhee ( <i>Pipilo fuscus</i> ).....	1	1.15	1	1.11
Subtotal birds.....	2	2.30	2	2.22
Red-headed skink ( <i>Eumeces gilberti</i> ).....	0	0.00	2	2.22
Side-blotch lizard ( <i>Uta stansburiana</i> ).....	3	3.45	2	2.22
Fence lizard ( <i>Sceloporus occidentalis</i> ).....	4	4.60	3	3.33
Whiptail lizard ( <i>Cnemidophorus tigris</i> ).....	2	2.30	2	2.22
Spadefoot toad ( <i>Scaphiopus hammondi</i> ).....	2	2.30	0	0.00
Subtotal reptiles and amphibians.....	11	12.64	9	10.00
Grand Total.....	87	100.00	90	100.00

Fitch (1949a, p. 547) later added over 100 more records, and at the same time translated the data into the proportionate weight represented by each species of prey. He reached the following conclusions: Mammals comprise 98.3 per cent of the food of the rattlesnakes on the Range, birds 0.7, and amphibians and reptiles 1.0 per cent by weight. The only species constituting over 1.0 per cent are ground squirrels 68.8, cottontails 17.3, kangaroo rats 5.5, pocket gophers 2.5, and wood rats 1.7. But Fitch points out (p. 549) that certain kinds of food—the smallest species of mice (such as *Perognathus inornatus*) and the lizards—although composing only 2½ per cent of the food by weight, are nevertheless highly important since they are the only prey that the very young snakes can successfully swallow.

The comments of Fitch and Twining (1946, p. 68) on the sizes of snakes favoring different kinds of prey are of interest:

Small snakes, less than a year old, with head and body lengths less than 18 inches and without more than 3 rattles, had eaten one of the 8 pocket gophers, one of the 5 kangaroo rats, 6 of the 9 pocket mice, 7 of the 10 *Peromyscus*, 2 of the 4 fence lizards, both of the whip-tails, the 3 brown-shouldered lizards, and both of the spadefoot toads.

Rabbits, ground squirrels, wood rats, and quail are the main food of the large snakes. Gophers, kangaroo rats, meadow mice, larger lizards, are eaten mainly by middle-sized individuals, which likewise may occasionally take a small squirrel or rabbit, or any of the food items taken by the small snakes. Mice, small lizards, and spadefoot toads comprise the food of the smallest ones during the period when growth is most rapid.

With respect to the ground squirrels, Fitch and Twining point out that all of those eaten were young-of-the-year, and all were eaten by adult snakes having a head plus body length in excess of 2 feet. Nine out of 10 of the rabbits, and 20 out of 23 of the squirrels were, in fact, eaten by snakes exceeding 28 inches in length. By summer the young squirrels have grown to such an extent that they are beyond the capacity of any but the very largest snakes.

Some other published records of mammal prey eaten by the northern Pacific rattlesnake are as follows: Evermann (1915, p. 1)—Merriam chipmunk (*Eutamias merriami*); Bryant (1925, p. 72)—wood rat (*Neotoma*); Gilmore (1934, p. 70)—Yosemite pika or cony (*Ochotona schisticeps muiri*); Fitch (1936, p. 651)—dusky-footed wood rat (*Neotoma fuscipes*) and meadow mouse (*Microtus*); Hubbard (1941, p. 206)—dusky-footed wood rat (*Neotoma fuscipes*), and California brush mouse (*Peromyscus boylii boylii*). Evans and Holdenried (1943, p. 243) reported that, out of 14 northern Pacific rattlers examined, 4 had eaten young California ground squirrels (*Citellus b. beecheyi*). Fitch and Glading (1947, p. 104) give the same list of mammals as Fitch and Twining (1946), and a further discussion is contained in Fitch (1948a, p. 589; 1948b, p. 28; and 1949a, p. 548). Linsdale and Tevis (1951, p. 182) tell of the heavy inroads made by these rattlers on the population of the Santa Lucia dusky-footed wood rat (*Neotoma fuscipes luciana*) on the Hastings Reservation in the Santa Lucia Mountains of California.

A number of my correspondents have mentioned special items of mammal prey taken by northern Pacific rattlesnakes:

The largest prey that I have seen being swallowed was a half-grown Oregon snowshoe rabbit.<sup>11</sup> E. J. Parker, U. S. Forest Service, Ukiah, Oreg.

<sup>11</sup> *Lepus washingtoni klamathensis*.

On one occasion I found a northern Pacific rattlesnake feeding. It was a snake about 12 inches long that I came upon in the daytime in the Santa Cruz Mountains. It had in its mouth a California shrew-mole (*Neurotrichus gibbsi hyacinthinus*) which is an uncommon animal. Anita Daugherty, California State Fisheries Laboratory, Terminal Island, Calif.

Records of northern Pacific rattlesnakes that have preyed on birds are not numerous. The observations of Fitch and Twining (1946, p. 65) have been mentioned already. Various observers have given me the following data on ornithological prey:

One afternoon when out for a walk, I saw my dog made a sudden swerve and, on approaching the spot, was at first entirely puzzled. A bird, with outstretched wings, was steadily approaching me tail first. I then saw that a rattler had begun to swallow it head first, but had been unable to complete the process by reason of the outspread wings, preventing the passage of his victim—a Gambel sparrow<sup>12</sup>—farther than the shoulders.

On another occasion a hen Richardson grouse<sup>13</sup> was seen to be in a state of great agitation. She refused to fly away at my approach and I saw, close by, a chick still warm. Thinking it to be the victim of a weasel, I looked for the culprit and seeing something chequered lying concealed in a tuft of grass, I stooped down to pick it up, when I saw a rattlesnake wriggling away. When I skinned the chick two hours later, decomposition had so far advanced that one wing fell off. A. C. Mackie, Vernon, B. C.



Lookout Alfred H. Barnum on Deadwood Mountain saw a bunch of grouse<sup>14</sup> scurry away from a bush one day and observed that one fell flapping to the ground within a few feet. He came down from his 20-foot tower to examine it and found it dead. When he went back to the bush to investigate, he found a big rattler, which he killed. There were three bloody slits in the side of the grouse, showing where it had been struck. These grouse are about the size of mountain quail. George S. James, U. S. Forest Service, Yreka, Calif.

Aside from the records of Fitch and Twining and their associates on the San Joaquin Experimental Range, in which four species of lizards and a spadefoot toad are shown to be included in the diet of the northern Pacific rattlesnake, not many herpetological food items have been called to my attention. Fitch (1940, p. 169) has mentioned a Yosemite fence lizard (*Sceloporus occidentalis taylori*) that was eaten, and it is known that the two more widely distributed subspecies (*S. o. occidentalis* and *S. o. biserialatus*) are important parts of the diet of young *oreganus* throughout its range. Insect remains (Coleoptera and Hymenoptera) were found in one young rattler, but as usual there were lizard scales, suggesting that the snake had not eaten the insects directly. A captive *oreganus* ate a leaf-nosed snake (*Phyllorhynchus decurtatus*). Hathcock (1937, p. 339) showed a photograph of one captive *oreganus* that was eating another.

*Ridge-Nosed Rattlesnake* (*C. willardi*).—Van Denburgh (1922, p. 961) reported a specimen of the Arizona subspecies that had eaten an adult mouse. I have noted one containing mammal hair, and another, a juvenile 248 mm. long, that had eaten a spiny lizard, probably *Sceloporus j. jarrovi*. No doubt, as is the case with other rattlers of small size, lizards comprise a major element of diet of *C. w. willardi*, especially of the young. Kauffeld (1943a, p. 345) fed white mice to a captive specimen. Vorhies (1948, p. 302) found that they ate lizards readily in captivity; also one ate a spotted night snake (*Hypsiglena*) about as long as itself. Woodin (1953,

<sup>12</sup> *Zonotrichia leucophrys gambeli*.

<sup>13</sup> *Dendragapus obscurus richardsoni*.

<sup>14</sup> Sooty grouse (*Dendragapus obscurus fuliginosus*).

p. 295) observed that *willardi* would eat lizards in captivity; they were accepted when dead. One *willardi* was found to contain a brush mouse (*Peromyscus boylii*). A. E. Ball wrote me that a ridge-nosed rattler disgorged a scorpion about two inches long. The food of the other two subspecies of *willardi* is probably the same as that of the nominate subspecies. Two specimens of the Chihuahuan ridge-nose (*C. w. silus*) contained mammal remains, and another an alligator lizard (*Elgaria kingi*). Lowe and Marshall (*in litt.*) found one that had eaten a pileolated warbler (*Vilsonia pusilla*). A specimen of the southern ridge-nose (*C. w. meridionalis*) had eaten a mouse.

*Eastern Massasauga* (*S. c. catenatus*).—This is the largest rattlesnake of the genus *Sistrurus*, which comprises the rattlesnakes having plates, rather than scales, on the anterior part of the top of the head. According to Netting (1932, p. 11) the massasauga feeds on rats, mice, birds, and frogs. It seems to feed on frogs more consistently than any other rattlesnake whose food habits are equally well known. In some areas it inhabits marshy ground, which probably accounts for its propensity for amphibians. Evermann and Clark (1914, p. 348) state that it feeds on frogs, crawfish, meadow mice, and shrews, and probably on fish.

The following data are taken from published accounts of this rattlesnake: Taylor (1892a, p. 752; 1892b, p. 357), from his examinations of stomach contents, believed it to be largely a mammal feeder. Atkinson and Netting (1927, p. 42) and Lyon and Bishop (1936, p. 254), each report specimens that had eaten meadow mice (*Microtus pennsylvanicus*). Wright (1941, p. 668) found a specimen containing a northern white-footed mouse (*Peromyscus leucopus noveboracensis*); another contained a field mouse. As to birds, Netting (1927, p. 26; 1932, p. 11) lists them among the food of this snake, but I have no data on the particular species eaten.

Ruthven (1911, p. 270; also Ruthven, Thompson, and Thompson, 1912, p. 124; Ruthven, Thompson, and Gaige, 1928, p. 132) mentions two instances in which massasaugas ate snakes, both of which had probably been found dead when they were eaten. One of the snakes was another rattler; the other could not be identified. The same authors concluded that, in Michigan, frogs comprise the bulk of the food of this rattlesnake. Atkinson and Netting (1927, p. 42) reported the finding of spring peepers (*Hyla crucifer*) in specimens collected in the wild. LeRay (1930, p. 203) saw one that was feeding on a leopard frog (*Rana pipiens*). From its appearance he thought the frog might have been dead when the snake found it. Netting (1932, p. 11) says the massasauga eats other frogs besides spring peepers and leopard frogs. Fox (1948, p. 66) found one containing a large frog.

As to feeding in captivity, Ditmars (1912, p. 231) said massasaugas as readily eat frogs as small mammals or birds. They usually retained hold of cold-blooded prey, but dropped mammals after the strike. Atkinson and Netting (1927, p. 42) fed captive specimens with half-grown leopard frogs. Curran (1935, p. 338) says some captive specimens will eat nothing but frogs; but on the other hand Wright (1941, p. 668) tells us that his captives would eat only white-footed mice or field mice, even though frogs were also present. Loewen (1947, p. 53) kept a captive specimen nearly 14 years, during which time it ate mice, sparrows, chicks, lizards (2 race runners and a collared lizard), one young rabbit, a bat, a mole, and pieces of meat of various kinds.

*Western Massasauga* (*S. c. tergeminus*).—The western subspecies of the massasauga probably has much the same food habits as the eastern. From the character of the country it inhabits, it may be expected to be more of a lizard- and less of a frog-eater than its eastern counterpart. One Oklahoma specimen contained a whiptail lizard.

*Pigmy Rattlesnake* (*S. miliarius*).—Conant and Bridges (1939, p. 143) state that this species feeds on mice, young birds, small frogs, lizards, snakes, and insects. Necessarily the diet is circumscribed by its small size. Davis and Brimley (1944, p. 9) add baby rats to the menu. Specific food records are few. Wright and Bishop (1915, p. 189) found the remains of a small snake or lizard in the stomach of one, and a brown skink (*Leiolopisma laterale*) in another. These items pertained to the southeastern subspecies (*S. m. barbouri*). Allen and Neill (1950b, p. 10) say that the young of this subspecies prefer slender lizards (*Anolis*); the adults eat frogs, lizards, ribbon snakes, young water snakes, and sometimes the young of their own subspecies.

I found mammal hair in an individual of the western subspecies (*S. m. streckeri*) from Avery Island, Louisiana. Halter (1915, p. 60) reported that a garter snake was swallowed by a pigmy rattler in captivity. Clark (1949, p. 260) examined the stomach contents of 11 rattlers of this subspecies and found that they had eaten frogs (*Rana clamitans*, *R. pipiens sphenocephala*, and *Acris*) as well as an unidentified bird. The food of the Carolina subspecies includes mice, lizards, small snakes, and centipedes (Hamilton and Pollack, 1955, p. 3).

*Mexican Pigmy Rattlesnake* (*S. ravus*).—I found mammal remains in two specimens, and lizard scales in another. One lizard of the genus *Mabuya* was found to have been eaten. Davis and Smith (1953, p. 142) report that a captive specimen ate a spiny lizard (*Sceloporus torquatus*). I was told by John E. Werler that captive specimens prefer lizards as food.

## METHODS OF SECURING PREY

If there is any predominant method by which the rattlesnake secures its prey, it is this: He lies in wait by a trail along which some small animal is likely to pass. Aided by a keen sense of smell, a heat receptor (the facial pit), and, to a lesser extent, by sight, he becomes aware of a passing mammal. He makes a forward-lunging strike at the prey. At the end of the stroke his fangs seem barely to touch the victim. The head is drawn back and the snake waits. The bitten prey stumbles forward on its way for a few feet, or maybe for several yards, if it be large or the strike has not been fully effective. The victim seems to hesitate uncertainly, then loses control of its movements. A few convulsive kicks and it is dead, only a few seconds or, at most, some minutes after the fatal stroke; for the venom injection is large in proportion to the bulk of so small a creature. Meanwhile the rattler, after waiting for a short time, uses the sense of smell to follow along the course taken by the stricken animal. Reaching it, he carefully touches it here and there with his tongue, as if to find whether there remains any danger of a retaliatory bite or struggle. Finally, he seizes it by the nose and the actual swallowing proceeds.

## THE PURPOSE OF VENOM

Of course, on this simple pattern there are many variations, as dictated by the particular conditions under which the prey is found, and its nature as well. But primarily it is to be noted that the prey is bitten and dies from the venom, for a snake's poison is essentially a means of securing food. As a protection against larger enemies it may have value, but it is to be doubted whether this phase was important in the evolution of the poison mechanism of snakes.

Some writers of bygone days (e.g., Lombard, 1881, p. 88) have questioned whether poisonous snakes—rattlers among them—bite and inject venom into their prey, for it was thought that poisoning the prey would render it unfit for food. S., E. (1883, p. 7) claimed that he saw a rattlesnake swallow a bird up to the point where it had been bitten, but upon reaching this poisoned section the snake stopped and threw it up. But modern studies, both in the field and laboratory, have left no doubt concerning this purpose and use of the venom; and as to a possible detrimental effect on the swallower, it should be observed that venom is virtually harmless when taken internally—it must enter the blood stream to be injurious. The theory that the deteriorating effect of venom on the tissues of the prey actually aids in digestion, a theory long ago advanced by Fontana (1787, vol. 1, p. 63), is now generally accepted (see also p. 777). The protective value of the venom, in making it unnecessary to hold onto and subdue a struggling creature that might injure the snake, was also early recognized (Labat, 1722, vol. 4, p. 106; Sloan, 1734, p. 331; Watson, 1754, p. 286). Thatcher (1940, p. 36) cites the fact that tame rattlers in captivity will strike their prey, but not the persons who handle them, as another proof that the purpose of the venom is food procurement rather than defense.

## CHARMING PREY

For a long time it was believed that snakes—rattlesnakes particularly—had the ability to charm or fascinate their prey. It was thought that a rattler had only to lie under a tree and to flash its glittering glance upward at some innocent bird or squirrel, whereupon the poor creature would inexorably flutter or run down into the waiting jaws. Although particularly current in the eighteenth century, belief in this power of fascination is still widespread today. It has been denied by scientific investigators since the earliest times, and has failed of verification by herpetologists after extensive observations of rattlesnakes both in the field and in captivity, yet it will not down. I have discussed the theory of fascination more completely in chapter 18.

## AMBUSHING PREY

Most observers are agreed that rattlesnakes secure their prey largely by lying in wait for it in likely places, especially beside trails or burrows. Any small animal passing within range is struck and thus secured. Fitch and Twining (1946, p. 65) have cited typical instances occurring on the San Joaquin Experimental Range:

On two different occasions the actual striking of a squirrel by a [northern Pacific] rattlesnake was seen in the field. In one observation, recorded by Raymond Sharp, the squirrel jumped from an overhanging flat rock and was struck by a snake which was lying coiled beneath. The squirrel was hit in the left shoulder, and ran about erratically bumping into objects in its path, then lay down with its sides jerking convulsively and its eyes shut.

Four minutes later when the observer approached, it escaped into a burrow entrance, reeling about and falling on its side as it moved. Another instance was observed when a young squirrel running to its burrow in alarm, passed near a large rattlesnake, which lashed out and struck it broadside, and was jerked out full-length before it could disengage its fangs. The squirrel squealed and scurried into its hole but probably it died soon afterwards.

Similar observations made by my own correspondents have been these:

I have seen rattlesnakes kill and eat chipmunks. They wait at a hole or along one of their runways. Then when one comes along they lunge and strike it. *Ed Rose, U. S. Fish and Wildlife Service, Chilcoat, Calif.*



Once another ranger and I were walking down a small ravine when a half-grown cottontail rabbit, some 20 feet from us, started to run, and was almost immediately struck by a large rattlesnake in our plain view. It did not rattle. The rabbit stopped within 8 feet and in 10 minutes it was dead. We waited some 15 minutes and cautiously crept up near where the snake had struck the rabbit, and saw it crawling slowly toward the dead rabbit. We climbed upon a rock that gave us a good view, and watched the swallowing process for some 15 minutes. The snake swallowed nearly one-half of the rabbit in that time. *L. E. Crawford, Superintendent of State Game Rangers, Lawton, Okla.*

Kalm (1752–53, p. 315) stated that timber rattlers frequented the banks of brooks in the hope of striking animals coming down to drink.

#### HUNTING IN HOLES

Many observers have happened upon rattlesnakes just as they were striking their prey, and more have found them engaged in swallowing it. But few, indeed, have taken the time to watch and record the methods used by a rattler when actively engaged in hunting. The best account of which I have knowledge is that of Tevis (1943, p. 242). This so completely describes the hunting methods of a rattlesnake under natural conditions that it deserves extensive quotation. The observation was made near El Rosario, Baja California, in June, 1941, when the rattler, a red diamond (*C. r. ruber*) was watched for two days. Tevis writes:

On June 5, at 10:20 A.M., a young squirrel appeared suddenly at my feet much frightened. Forty-five feet away I found a red rattlesnake, an individual 37 inches long with nine rattles. The body color was red-brown and the short tail was barred with alternating coal-black and light-gray rings. When the snake realized I was not pursuing, it coiled deliberately on the dried annuals beside an adjacent squirrel runway. It was difficult to see, for its color blended with the tawny color of the dried vegetation and the bright tail was hidden beneath the body. Had it coiled on the bare ground or on the green foliage and yellow flowers of the tarweed, or had it not hidden its tail, it would have been conspicuous.

The bark of an adult squirrel 50 feet distant was ignored. At 10:35 the sun broke through the fog; the air warmed rapidly. Twenty minutes later the snake pushed off through the vegetation, head raised, tongue flickering, and the vertical black rings of the tail in startling contrast to the vegetation. Coming to one of the five holes of a squirrel burrow it inserted its head for ten seconds while flickering the tongue against the walls, then withdrew to crawl along a runway to another hole partly covered by a cholla. After again inserting the head and flickering the tongue, the snake entered.

Three young squirrels suddenly and simultaneously hurtled out of a hole on the opposite side of the cholla. They were bewildered, nervous, and held their tails tightly over their backs. Even though they saw me, they would not return to the burrow, and ultimately they hid under vegetation.

Ten minutes later I located the snake; it was inside the shaded hole from which the squirrels had fled. Its neck was bent into an S-coil, and its head, facing outward at the entrance, was pressed against the ground, motionless, an excellent simulation of a brick-red

rock. For at least three and one-half hours the snake did not move. In other words, over the warmest part of the day it rested in shade at a spot that might yield food. Sometimes I saw the young squirrels. They stayed in the vicinity, barking, hiding under brush, and, peculiarly enough, running in and out of holes other than the one in which the snake rested.

By 3:24 P.M. the snake had moved 8 feet, and was now hidden among the dead annuals, neck in the S-coil, and head pressed onto the ground one inch from and facing a hole. A young squirrel frightened by me ran to the hole. The snake struck. Its jaws seized the squirrel by the hindquarters. The latter gave a single, shrill, somewhat choked scream, struggled for five seconds, then became quiet. Two minutes after the strike the snake relaxed but did not release its hold. The squirrel again struggled, weakly; only the front parts were able to move. As soon as the squirrel's rapid, forced breathing ceased, the snake began swallowing the hindquarters. Large gulps were separated by four- to five-second intervals of rest. After one minute the squirrel's hind feet disappeared between the jaws. For four minutes thereafter the snake yawned frequently, exposing the saliva-filled pink mouth and the loosely hanging flesh-sheathed fangs.

Instead of resting, it crawled off, apparently eager for more food. I was able to keep it in sight off and on for three-quarters of an hour. Although it was continually on the move and usually avoided bare spots, it never went outside a 25-foot circle that included the burrow system. Right-angled turns were frequent. Sometimes it pushed under vegetation only to withdraw and head in the opposite direction. Other times when under cover, it raised the anterior part of the body until the head was clear. Once it crawled over a bush to a height of a foot and a half above the ground. The ever-flicking tongue again and again quivered against stalks of dry annuals and touched objects, such as rocks. Bushes were probed with the head, the neck raised.

Whenever the snake came to a hole, the head was inserted for about ten seconds, and the tongue flickered against the wall. Twice after such an examination, the snake entered the hole to stay below ground for five or more minutes. Deliberate in its movements and ever intent and alert, the snake gave the impression of reconnoitering or searching. Undoubtedly it was trying to ascertain the whereabouts of the remaining squirrels. Noble and Schmidt (1937) found that blindfolded and tongueless crotalid snakes with unimpaired facial pits will strike at a freshly killed rat but not at a chilled rat, and conclude that crotalid snakes detect the body heat of their prey at a distance by means of the facial pits. Bogert (1941) found that a tongueless rattlesnake does not assume the defensive position it ordinarily does when confronted by certain odorous substances present in the integument of its enemy, the kingsnake, which shows that the tongue is used in the detection of odors. I assume that the snake I was watching inserted its head into the holes and flickered its tongue against the walls in order to determine by the presence or absence of body heat and odor whether or not a squirrel was below.

At 4:10 the fog returned. At 4:18 the air was cooling rapidly. At 4:45 the snake again entered one of the holes. Presumably it remained within, for I was not able to locate it until 11:15 A.M. the following day.

With the sun out in full force on June 6, the snake was coiled on dried vegetation in the shade of a bush not more than 20 feet from the spot where last seen. Because its body was swollen and because I did not see or hear a squirrel all day I concluded later that the snake had cleaned out the colony of young squirrels. At 2:55 P.M. it began reconnoitering movements as of the previous afternoon—circling, backtracking, examining objects, and inserting its head into holes—but, as would be expected if no squirrels remained and the snake by its investigation could tell whether or not a squirrel was below, it did not enter a hole. Once it inserted its head, flickered the tongue against the walls, withdrew the head, then seemingly unsatisfied, again inserted it. At 3:20 it curled its body around the base of a bush and rested, tongue inactive and head on the ground.

Thus we learn that rattlesnakes not only lie in ambush along trails where prey may be expected to pass, but actively search for food down burrows or in rock crevices in which animals are accustomed to seek refuge. The snakes are evidently

able to determine by scent whether a hole is likely to prove fruitful. Fitch (1949a, p. 518) even saw a northern Pacific rattler interested in fresh gopher mounds; it was pressing its snout into the soil as if trying to force its way in.

Hunting is thriftily combined with protection; a snake, while taking refuge in a mammal burrow from the sun or possible enemies, is advantageously located to make a meal of the owner. On the San Joaquin Range, Fitch (1948a, p. 591) found that ground-squirrel holes were the usual refuges of the northern Pacific rattlers, and in the late afternoons of the hot, dry summer, they might be seen lying just within the entrances, as if waiting for it to become cool enough to emerge.

Pack-rat nests are similarly used. A correspondent writes:

During the summer I saw a pack rat hastily leave its nest (mainly soil drift about a *Rhus trilobata*) at noon in the blazing sunlight. This seemed unusual until investigation revealed a large prairie rattler (*Crotalus v. viridis*) coiled in one of the entrances. The observation was made in Roosevelt County, New Mexico. *Philip F. Allan, Soil Conservation Service, Fort Worth, Tex.*

#### PREY STARTLED TOWARD SNAKES

While many animals are caught unawares by poised and waiting rattlers within whose striking range they pass, others are frightened into a fatal proximity by some other threat, a lurking coyote, for example, or a hovering hawk.

As the [ground] squirrel burrows are favorite hiding places for rattlesnakes, the squirrels are in constant danger of being bitten underground or in the burrow entrances. Although squirrels are alert and watchful for lurking snakes, accidents are frequent, and are most apt to happen when the squirrels are frightened to their burrows by some other danger and momentarily are off guard. Several such incidents were seen. Two young squirrels scared into the same hole when the observer approached popped out and back in again several times within a few seconds, and gave shrill squeals while underground. Then a small rattlesnake emerged from the hole, rattling and attempting to escape. Another time a large squirrel frightened into an apparently deserted burrow burst out again backwards and ran to another hole. Then a snake was heard rattling down in the burrow the squirrel had left. *Fitch and Twining, 1946, p. 67.*



I discovered a black-tailed rattlesnake (*C. m. molossus*) at the mouth of a hole in limestone. As I approached to catch the snake, a young gray squirrel 11 inches long, was frightened and attempted to run past the snake into a hole, but was struck by it. I caught the snake, which was 43 inches long. I found the dead squirrel about 12 feet away. It must have died in less than 5 minutes. *Homer F. Hastings, National Park Service, Camp Verde, Ariz.*

These are examples of how man himself may frighten some animal into passing too close to a waiting rattlesnake, an obvious reason why so many people have happened to see the prey stricken.

Snakes may lie in wait for birds as well as mammals. A. M. Jackley, while rattlesnake control officer of South Dakota, wrote:

Birds approach a rattler through curiosity, and oftentimes in that way become easy victims. This fall I saw a large rattler stretched out by the side of a prairie-dog hole, and I counted 11 horned larks gathered around him, some within easy striking distance. But he seemed fat and lazy, and paid little attention to them.

I have taken pictures of birds gathered around individual rattlers. The birds were horned larks, buntings, and meadow larks. I saw one bunting killed. When I see a meadow lark standing with his head raised high and gazing into the weeds, it is nearly certain he has a rattler spotted.

An experience reported by Dean E. Batchelder indicates that desert rattlesnakes may lie in wait for birds and other creatures near some source of water. He wrote:

I thought you might be interested to hear of a rattlesnake found to have eight birds, probably goldfinches, in its stomach. It was two and a half feet long. The snake was killed during the latter part of May, at a headquarters camp of the Metropolitan Aqueduct about 10 miles north of Desert Center, Riverside County, California. As part of the camp, a garden had been planted, with a lawn and bird bath or small fountain. In the desert this naturally attracted many birds. The snake had evidently lain in wait near the water. The birds were all swallowed beak first. [The snake, sent me for examination, proved to be a southwestern speckled rattler (*C. m. pyrrhus*).—L.M.K.]

#### PURSUING PREY

If the prey fails to come within striking range of a hungry rattlesnake, the snake will sometimes trail it, trying to get close enough for a strike. Fitch and Twining (1946, p. 66) mention such an occurrence. They first describe the actions of three young ground squirrels that issued from a burrow, two of them evidently having been injured by a northern Pacific rattlesnake (*C. v. oregonus*), within. They continue:

A three-foot rattlesnake emerged from the burrow and crawled slowly over the mound where the young squirrels had been. Obviously in search of prey, it was darting out its tongue continually, nosing over the ground from side to side apparently trying to pick up a scent. It moved over and around the mound, passing within a foot of the afflicted squirrel, which was still sitting in the same hunched position, but apparently the snake did not notice it. The squirrel had become lethargic, and did not notice the snake either. An adult squirrel had been perched on a rock about thirty feet away, giving the low musical chirps used by mother squirrels to warn their small and inexperienced young of approaching danger. This adult came hesitatingly toward the place where the young had been, encircling the rock outcrop where the burrows were, and moving around the base of a boulder, it suddenly came face to face with the rattlesnake at a distance of about two feet. The squirrel emitted a sharp chirp and flicked its tail, and its hair fluffed out. The snake's body was extended so the squirrel was well beyond its striking range. For a moment it lay motionless, watching the squirrel, then it began to crawl slowly forward with its head and the anterior part of its body drawn back ready to strike. It seemed to be trying to get within reach but the squirrel edged away warily. The squirrel was aggressive, however, and would jump back, then take several steps toward the snake. Once it approached within a foot of the snake's head, and once scurried away in sudden fright, but quickly returned.<sup>15</sup> It continually faced the snake and kept flicking its tail sidewise and giving low, vibrating chirps. The snake, without making any sudden movement, followed it up over the sloping rock surface, but was not in a position to strike effectively. The squirrel, backing away up over the boulder, appeared to be exercising excellent judgment in keeping just beyond striking range; its movements were tense and cautious, and its attention was concentrated on the snake, so that for many minutes it failed to notice the observer. Finally it took alarm and ran to another outcrop. The snake crawled around to the burrow where it had emerged and disappeared.

One wonders whether these actions of the adult squirrel might have been intended to lead the rattler away from the young. At any rate, it is evident that a rattler will sometimes trail after an animal which has not come within striking range.

Stillwell (1939, p. 16) claims that rattlesnakes use the rectilinear method of progression when stalking prey. This is doubtful as this is the slowest method of

<sup>15</sup> An action such as this would certainly have been interpreted as fascination by one not so familiar as were these authors with the actions of squirrels.

crawling. Our observations of captives indicate that they employ the more customary sinuous motion, which not only permits greater speed, but allows them to advance with head and neck drawn back for a strike, when they are getting within range. However they may use either rectilinear or concertina progression when they near the prey.

#### VARIABILITY IN THE EFFECT OF A BITE

Just as there is a great variability in the effects of snake bite on a human being, for reasons that I have listed in another section (p. 742), so also observers have noted differences in the results on prey. When we remember that the danger from a given quantity of snake venom is inversely proportional to the bulk or weight of the creature bitten, it might be supposed that rattlesnake bite would be quickly fatal to the small creatures on which they feed. While such is generally the case, there have been instances wherein stricken animals have been observed to cover considerable distances before succumbing, and others in which they have escaped and may have recovered.

This occasional ineffectiveness may be attributed to two particular causes affecting prey, among the many variables inherent in snake bite. First, it is to be remembered that rattlesnakes have full control over venom extrusion; they can, if they wish, bite without injecting venom at all. Their natural inclination is to conserve venom, since it is their means of food procurement, and it is possible that, in striking prey, they release much less than when under the stress and fear of defending themselves against some such large creature as man. Secondly, the very lack of bulk of the prey acts to the snake's disadvantage since the momentum of the strike carries the prey along, without the interposition of sufficient resistance to permit the fangs to be deeply imbedded. Of course, if the lower jaw is brought effectively into action, so that there is a viselike bite, rather than a simple stabbing of the fangs, then the latter will be fully imbedded. The strike is too rapid to determine by eye whether, when prey is struck, the lower jaw is used to bite against; we know that it is often so used when the snake strikes in anger (p. 830). Probably there is as much variability here as in other rattlesnake actions. At any rate, in watching rattlesnakes strike small mammals in captivity, one cannot but be impressed by what seems to be the lightness of the touch. Except for the effects of the venom one will frequently think that the snake has missed—as indeed it often does—for the target may not be appreciably moved by the blow.

Fitch and Twining (1946, p. 67), basing their opinion on the condition of rattlesnake prey found in the field, think the prey sometimes escapes, while in other instances it dies but a few feet from where it was struck. Two ground squirrels and a kangaroo rat were found to have only subcutaneous bites and probably died slowly; but another kangaroo rat had its thoracic cavity punctured, so death must have been almost immediate. One squirrel survived a bite in the thigh and axilla for an hour and three-quarters.

The following are quotations from the observations of some of my correspondents on the rapidity of venom action:

I have noted that mice usually die within a few seconds after being bitten, provided the rattler has had a good supply of venom. *Marion E. Rose, Pateros, Wash.*

I have seen animals weighing up to two pounds killed in their tracks by a single strike of a canebrake rattlesnake (*C. h. atricaudatus*), while others traveled considerable distances before paralysis stopped them. *E. A. Mcllhenny, Avery Island, La.*

#### UNEATEN PREY

That rattlesnake strikes are sometimes ineffectual, even though the prey be actually hit, is certainly true. However, one can never be sure the animal struck has really escaped injury, unless it be followed for a while to see if any delayed symptoms are manifest. Fitch and Twining (1946, pp. 65, 67; see also Fitch, 1948a, p. 591; 1949a, p. 550) have pointed out how considerable a number of creatures have been found dead in the field from rattlesnake bite, some because the rattler was unsuccessful in finding them after a strike, some because the snake was not hungry. These authors (p. 65) thus describe their experience with northern Pacific rattlesnakes on the San Joaquin Experimental Range, in California:

Many animals bitten by rattlesnakes are not eaten by them, and the snakes are much less inclined to rattle in the presence of small animals than in the presence of man or large animals which might trample them, causing death or injury. Rather, when approached by a rodent, the snake is apt to strike without warning. The bitten animal may be too large to be swallowed, or it may run too far for the snake to follow or may die in some inaccessible place, or the snake may not be sufficiently hungry even to attempt trailing it. The number of prey animals killed in this way but not used perhaps exceeds the number actually eaten.

However, these writers record only eight ground squirrels and six kangaroo rats, killed by snake bite, that were subsequently found uneaten in the field.

Although there is no question that some animals do escape and recover through ineffectual strikes, stories of animals held in rattlers' mouths that are later found to be unhurt are generally to be discounted, for the struggles of such a creature would incite a rattler to bite effectively. Thus we may doubt the two experiences reported by Kendall (1892, p. 588) wherein he liberated, unhurt, both a quail and a rabbit held in the mouth by diamondbacks that he had shot. Cranston (1913, p. 462) tells an even more fantastic story of how he watched a large rattler strike a rabbit again and again without effect. Finally the rattler lost its balance and fell off a ledge, whereupon the rabbit ran away.

#### DIFFERENCES IN DEALING WITH PREY

Although exceptions have been noted, there seems no doubt that rattlesnakes usually release a mammal which has been bitten but retain hold of a bird, reptile, or amphibian. In explanation of these differences it may be presumed that the mammal is released to avoid the danger of a retaliatory bite; the snake can readily follow its scent to the place where it dies and thus will seldom lose its prey. But this would not be true of a bird that might fly a short distance and be lost;<sup>16</sup> or of reptiles and amphibians, on which venom acts more slowly so that they might die too far away to find. Also, the retention of a hold permits a bite, rather than merely a stab, and hence a greater assurance of venom injection.

<sup>16</sup> Quemada Grande Island off the coast of Brazil is a landing place for migrating birds that stop for rest and food. They are preyed upon by a small pit viper (*Bothrops insularis*) that awaits them concealed amid the foliage of the trees. When a bird alights within reach, the snake lunges forward and strikes. It seldom drops the bird, but holds fast to prevent its escape, and at the same time grips a branch with its tail to avoid falling (summarized from Amaral, 1921, p. 85).

As early as 1722, Labat (vol. 4, p. 106; Sloane, 1734, p. 331) voiced the theory that snakes bite their prey and then release it to avoid injury; afterward they approach it again when it is safely dead. There has been much confirmatory evidence of differences in the actions of rattlesnakes toward mammals as compared with other prey, although occasional exceptions have been observed. Ditmars (1912, p. 231) reported that the massasauga (*Sistrurus catenatus*) held on to cold-blooded prey, but not to warm-blooded prey. Russell (1926, p. 107) said that a northern Pacific rattlesnake would barely touch a deer mouse in a strike. The mouse first scampered away as if unhurt, yet would die in about 40 seconds. Gloyd (1937, p. 127) fed mice to a banded rock rattlesnake. One, after striking a mouse in the usual way, followed it up at once, and seized and held it until all struggles ceased. Thatcher (1940, p. 38) tells of a rattler that struck a sparrow and held on. La Rivers observed how a Great Basin rattler (*C. v. lutosus*) seized and held a leopard frog; and Clark (1949, p. 260) observed that western pigmy rattlesnakes (*S. m. streckeri*) did not release frogs that they had struck. Falck (1940, p. 135) made the following observation on the mottled rock rattlesnake (*C. l. lepidus*) in captivity:

When amphibians were taken, the snake deliberately grasped the food animal, retaining it in its jaws, and by means of chewing motions imbedded the fangs as deeply as possible. The procedure was very different in taking mammals. Mice were invariably not retained in the mouth, death occurring rapidly. The snake eagerly followed its dying prey, which only occasionally reached even the opposite side of the cage before collapsing. The action of the venom was clearly more rapid in mice than in frogs and salamanders.

Tevis (1943, pp. 243, 245) watched a red diamond rattler strike and eat a young ground squirrel and also a kangaroo rat that was thrown toward it. In one case the prey was not released after being struck but was swallowed at once. Minton (1944, p. 476) reports that timber rattlesnakes (*C. h. horridus*) in captivity made the usual differentiation between rodents and birds, for the former were struck and released, while the latter were held despite their struggles. Marcy (1945, p. 170) reported on the feeding habits of a brood of the Mexican west-coast rattlesnake (*C. b. basiliscus*). When mice were struck the little rattlers sometimes held on while the mouse made several jumps. This temporary holding resulted in a more quickly fatal bite, usually within 30 seconds. McCauley (1945, p. 137) states that, whereas mammal prey is usually released by timber rattlesnakes, one that seized a half-grown robin held it clear of the floor of the cage and did not let go until it ceased to flutter. It was then laid on the floor and was touched tentatively with the tongue and sniffed before being swallowed.

Fitch and Twining (1946, p. 65) saw two ground squirrels struck by northern Pacific rattlesnakes in the field; in both cases the squirrels were immediately released. But they report a different action in the case of a California quail (*Lophortyx californica*):

On one occasion a flushed covey of quail consisting of parent birds and nearly-grown young lit in thick brush, and immediately loud distress calls and fluttering were heard. The observer hurried to the spot and found a quail struggling feebly, anchored down by a large rattlesnake, whose fangs were deeply imbedded high on one side of the quail's breast. In a few seconds the quail's head drooped and its breathing became convulsive; in four minutes its movements ceased and it appeared to be dead. Three and a half minutes

later the snake released it and began nosing over the limp body, occasionally opening its mouth to grasp the quail hesitantly. These actions continued for about sixteen minutes . . . until finally it seized the head and began swallowing.

That rattlesnakes may occasionally be injured by their prey, despite the habit of releasing mammals, has been shown by Fitch and Glading (1927, p. 121), who report the case of a rattlesnake turned loose one day and recaptured the next. This was in connection with their program of marking rattlesnakes to study growth. During the one-day interval between captures, this snake had caught and eaten a pocket gopher, and, in so doing, sustained bites on the anterior part of the body. The bites were not serious, for the wounds were healing when the snake was again captured a week later.

At the San Diego Zoo our captive rattlesnakes are almost always fed on mammals and therefore we have not observed these differences between the methods of handling them as compared with birds and reptiles. We have observed that the dead mammals that are customarily offered the snakes are as often held as released after they are seized, but this may have resulted from a change in the snakes' feeding pattern caused by their being given dead prey only. The animal offered is often grabbed without being struck or deliberately bitten at all. Although prey taken in this way is usually dropped and sniffed preparatory to the securing of a hold advantageous for swallowing, this is not always done. Atkinson and Netting (1927, p. 42) fed leopard frogs to massasaugas in captivity and observed that they took them from a forceps and swallowed them directly just as a garter snake would.

When rattlesnakes are engaged in robbing a nest of helpless young mammals or birds, they seem to sense the fact that the prey cannot escape; they consequently do not strike it, but merely seize and swallow one after another until all have been consumed. Several of my correspondents have observed this method of feeding.

#### INACCURATE STRIKES

One observation that every keeper of captive rattlesnakes eventually makes is the frequent and marked inaccuracy of some of the strikes. Even when alone and hence not confused by moving objects other than the prey, the snake may miss it either by misdirection or falling short. When excited by the odor of food, and there are other rattlers moving about the cage, they often become hopelessly confused, and strike at anything that moves. Fitch and Glading (1947, p. 121) cite the case of a dead northern Pacific rattler found near a mating pair. They hazard the guess that it may have been accidentally bitten as the result of an inaccurate strike at food by one of the other snakes; at any rate, there was no question but that it had died of snake bite, the fangs having punctured a vital organ.

#### SENSES USED IN SECURING PREY

The three senses used by rattlesnakes in finding, striking, and then recovering prey are sight, smell, and thermoreception (the pit).

Webb (1888, p. 270) expressed the belief that snakes follow their victims by scent. Baumann (1929, p. 36), in an important series of experiments, showed that European vipers follow females, as well as their prey, by scent or chemoreception. Kahmann (1932, p. 194; 1934, p. 249) also investigated the senses used in trailing. Neither Baumann nor Kahmann experimented with rattlesnakes.

Noble and A. Schmidt (1937, p. 263) were the first to solve the problem of the purpose of the facial pit of rattlesnakes—as well as other pit vipers. They proved that the pit is a heat receptor which permits a snake to locate and to strike objects that have a higher temperature than their surroundings, as is the case with warm-blooded prey, that is, mammals and birds. I have discussed rattlesnake senses elsewhere. Suffice it to say that, when they lie in wait for prey, all three senses may be used to detect its presence, the pit being the most important. When they seek prey in holes, rattlers undoubtedly depend on scent, as indicated by the observations of Tevis (1943) already quoted. The strike is guided by sight, and in the case of warm-blooded prey, by the pit. To find the prey after it has been struck and released, the snake depends on scent, although the pit may be useful if the snake is near the prey and the latter has not yet cooled.

In one case that Tevis observed, the snake went directly to a rat four feet away. Most reports agree that rattlers have little difficulty in searching out mammals that have been struck and released to die. Yet Fitch and Twining (1946, p. 66), in the citation already quoted, mention the case of a young ground squirrel that had been bitten, which the rattler seemed unable to find, although he passed within a foot of it while trailing it. Possibly he would have located it eventually had his attention not been drawn off by an adult squirrel that came within his recognition range. A lack of ability to find the prey, rather than lack of hunger, may account for some of the bitten but uneaten animals found in the field.

A number of observers have recorded the actions of rattlers that were trailing mammal prey which had been struck and then released. The snakes are described as being alert but unhurried, sensing their way along the trail of the stricken prey with flickering tongue, for they follow by chemoreception, in which the tongue plays an important role that supplements the sense of smell. We may strongly discount Allison's description (1946, p. 114) of a diamondback on the trail of a rabbit. The snake held its head up and waved it from side to side, and from its open mouth there came a strange humming sound.

#### CONSTRICTION

Although several of my correspondents have written of seeing rattlesnakes constrict their prey, I am disposed to doubt the accuracy of these observations. For, in the thousands of times that C. B. Perkins and others have observed rattlers in the course of being fed at the San Diego Zoo, no rattler has been seen to use this method. Dugès (1879, p. 16), who made detailed observations of captive rattlesnakes in Mexico, said one of his friends claimed to have seen a rat constricted by a rattlesnake, but this was contrary to his own experience. Langford and Gibson (1952, p. 115) reported the constriction of a rabbit. Constriction is, of course, a customary way of holding and subduing prey used by many kinds of snakes, but is not needed by those having the powerful alternative, venom. Rattlers, while swallowing prey, do not even steady or hold it down with a part of the body, as is the practice of some of the racers. They do, however, form a loop in the neck and drag the prey backward, as mentioned by Tevis (1943, p. 245), and by Fitch and Twining (1946, p. 65) in describing the eating of a quail. This method of eating, in which the head and a short section of neck face backward along the major length of the snake's body (which slowly advances forward), is characteristic of

many snakes, constrictors as well as nonconstrictors. Sometimes a rattler will take his prey to the shade of a bush before swallowing it (Fitch and Twining, p. 67).

One of my correspondents mentions that he found, in a rattler's stomach, a rabbit that he thought was both longer and slimmer than a normal rabbit, from which he judged it had been constricted before being swallowed. This is in reality a usual condition of prey, caused by the swallowing process as well as by partial digestion; it may be one source of the widespread belief that rattlesnakes constrict their prey.

#### METHOD OF SWALLOWING

The size of prey that any snake—rattlesnakes included—can successfully engulf, is a constant source of astonishment, especially because a snake can neither chew nor dismember its food but must swallow it whole, and must accomplish this unaided by either hands or feet. It is made possible by the elastic nature of the jaws and throat, and particularly by the fact that the halves of the lower jaw are flexibly attached to each other at the front, rather than being rigidly united as in lizards and mammals. Also, the bones of the jaws are thin and pliable. This elasticity of the whole structure allows distension of the mouth aperture, while the partial independence of the jaw sections permits the advancement and retraction of each half separately. Each is equipped with fine, curved teeth, whose points are directed backward; they comprise, in effect, four rows of hooks, each of which may be independently advanced, imbedded in the prey, and then pulled back, dragging the food with it toward the gullet. One or two half-jaws are advanced while the others hold the prey to prevent it from slipping out of the mouth. Thus, by a properly synchronized series of ratchet-like motions, the snake pulls the prey in, past the stretched constriction of the mouth and throat. Once past the point of narrowest opening, a series of lateral undulations of the throat is used to force the food down the gullet into the stomach.

As shown by X rays (figs. 9:1 and 9:2), taken by C. M. Bogert, of a rattlesnake as it swallowed a hamster, the jaw and throat distension is made possible by a lateral (outward) spread of the angle of the jaw (the point of connection between the articular and the quadrate) as well as by the vertical gape. The quadrate becomes almost perpendicular to the axis of the head, and the tabular (squamosal) also moves outward, posteriorly. There is no separation between the articular and the quadrate at the hinge, as has sometimes been supposed (fig. 9:1). But the attachment of the pterygoids at this point is less fixed, allowing some freedom of movement to the rows of short teeth in the upper jaw. Distally, the two mandibles are quite independent of each other, and it is in this bilateral independence that snakes have the greatest gain in engulfing power, both in the distension permitted and in the independent ratchet action of the two sides of the jaw.

The process of swallowing is thus described by one of my correspondents:

When a rattler eats a mouse, he swallows it head first, working first one side of the jaw over the mouse, and then the other, until the mouse is out of sight. Then the snake squirms to drive the mouse down his throat. *Gustave W. Koski, U. S. Fish and Wildlife Service, Windham, Mont.*

Several of my correspondents have commented on the surprisingly large prey that rattlers have been able to cope with successfully.

I found a Great Basin rattlesnake shortly after he had swallowed a Columbian ground squirrel. The snake was very lazy and swelled up around the squirrel. It was hard to see how he could have got it through his jaws. *J. W. Stokes, U. S. Forest Service, Ogden, Utah.*



Last summer, as I was driving along a mountain road, I saw a northern Pacific rattlesnake and stopped to kill him. He was medium-sized and had a large chipmunk about half swallowed. The chipmunk was bigger around than the snake, and how he ever stretched enough to get him half-way down I don't know. *Roy Bartholomew, U. S. Fish and Wildlife Service, Orland, Calif.*



Figs. 9:1 and 9:2. X rays of a red diamond rattlesnake (*C. r. ruber*) swallowing a hamster. The jaw and throat distension is made possible in part by the lateral outward spread of the angle of the jaw, as will be noted by the relative positions of the point of connection between the articular and quadrate during (upper figure) and after swallowing (lower figure). (X rays through the courtesy of Charles M. Bogert, American Museum of Natural History, New York.)

My own notebooks contain frequent mention of the surprising size of prey found in snakes. For example, a northern Pacific rattler only 15 inches long and  $\frac{3}{16}$  inch across the head at the widest part—the angle of the mouth—had swallowed a large mouse. When only the result was considered, the feat seemed impossible. Another juvenile had swallowed a full-grown whiptail lizard (*Cnemidophorus tigris*).

In swallowing large and difficult prey, rattlesnakes have one advantage over nonviperine snakes; they can and do use their fangs as hooks to aid the small, solid teeth in dragging the prey into the throat. I had the privilege of seeing a motion

picture, taken by Dr. C. T. Vorhies, which showed western diamond rattlesnakes in the act of swallowing cottontails, and this use of the fangs was clearly evident. When not in use the fangs lie folded up against the roof of the mouth. When it is desired to use them, either for biting or to draw in prey, the maxillary bone to which each fang is attached is rotated so that the fang swings downward and forward until its base is perpendicular to the roof of the mouth. The two fangs, one on each side, can be manipulated independently. By this means, first one and then the other is hooked into the animal being swallowed, and then each is both rotated and drawn back so as to pull the animal in. The fangs are more effective than the solid teeth because of their ability to rotate and also because their much greater length insures engagement through hair or feathers. Vorhies (1936b, p. 104) has mentioned this use of the fangs by the western diamond rattler (*C. atrox*), and Cook (1943, p. 52) by the eastern diamond (*C. adamanteus*). C. B. Perkins tells me this is quite usual with rattlesnakes, basing his statement on his observations of captives. Sometimes a rattler, if it has trouble in swallowing a large animal, will rub the prey against the ground or a rock; this helps to release a leg or wing that may have become caught in the angle of the snake's mouth.

The length of time required to swallow prey depends on the relative sizes of prey and snake. A small mammal may be swallowed in a minute or less, while a large one may require an hour or more. In the case of large and difficult victims, the snake will be seen to tire, taking lengthening rests between the rhythmical ratchet movements of the jaws. At the San Diego Zoo, where the snakes are never fed prey large enough to strain their jaws, the time required for swallowing has been found to vary from 3½ to 18 minutes, provided, however, that the snake swallows the prey head first, and so avoids the difficulties involved in other holds. The average swallowing time in 50 feedings of rattlesnakes of several species, recorded by Charles E. Shaw at the San Diego Zoo, was 7.6 minutes.

The following are observations by some of my correspondents on swallowing methods:

The only time I have seen a rattlesnake eating was in North Carolina on the Pisgah National Forest. A large timber rattler had a half-grown rabbit half swallowed and I would say it required approximately two hours before he had it completely swallowed. *T. S. Seely, U. S. Forest Service, Talladega, Ala.*



On Muddy Mountain in Natrona County, Wyoming, I watched a rattler eating a squirrel. It took the snake about two and a half hours to swallow it. *Fred W. Barnes, U. S. Fish and Wildlife Service, Hines, Oreg.*



A rattler will down a mouse in 5 minutes, but a robin is swallowed more slowly. *Marion E. Rose, Pateros, Wash.*

Kunzé (1879, p. 332) noted that it took a four-foot timber rattler (*C. h. horridus*) six minutes to swallow a large mouse, and four minutes for a small one. Wright (1941, p. 668) reported that an adult massasauga (*S. catenatus*) required about 15 minutes to swallow an adult meadow mouse (*Microtus*). Fenley (1940, p. 4) says it took 95 minutes for a western diamond to swallow a rabbit.

Lombard (1881, p. 88) claimed to have seen a timber rattlesnake take more than a day to swallow a rabbit; however, obvious inaccuracies in his statements on other rattler habits justify our doubting this observation. Equally doubtful are

statements by Browning (1860, p. 375, but writing as of 1800) that it took a rattler seven days to swallow a medium-sized woodchuck; also that a rattler, while eating a bird, held onto a bush with its tail (p. 373). It has even been said (e.g., Kalm, 1752–53, p. 59) that rattlers, in dealing with unusually large prey, may swallow it part way, and then wait several days for digestion to dispose of this portion before they complete the swallowing process. This is impossible since the anterior part of the prey would not reach the snake's stomach where digestion could proceed.

Even when a rattler holds its mammal prey, instead of letting it run until it dies after a strike, the snake will often drop it and nose it carefully before beginning the swallowing process. This is evidently for the purpose of getting an advantageous hold of the creature's snout or head so as to facilitate swallowing, for prey is usually swallowed head first. The head-hold reduces the impediment to swallowing imposed by hair and limbs. Most often a side of the prey is upward, rather than its back. Sometimes a snake will take two or three tentative holds before securing one that seems satisfactory. Even so, owing either to the eagerness of hunger or to an inability to recognize the head, a mid-body hold is sometimes taken. This makes it necessary for the snake, either to double the body of the prey, or laboriously to transfer the hold, by lateral movements of the snake's jaws, to the head of the prey. Occasionally animals are swallowed tail first, which also increases the difficulty. Such improper holds are not infrequently observed at the zoo. Some published accounts of animals eaten tail first will be found in Evermann (1915, p. 1), Ruthling (1916, p. 28), Kauffeld (1943b, p. 611), and McCauley (1945, p. 137). Waterton (1834, p. 67) scoffed at Audubon (1827, p. 22) for having maintained that he saw a rattler swallow a squirrel tail first; in this instance Audubon did not deserve the criticism. Kunzé (1879, p. 332), when he fed mice to a captive *horridus*, noted that one out of 40 was eaten tail first.

After a snake has swallowed its prey, it will usually yawn as if to relieve the stretched mouth parts and settle them again into a comfortable position. During this action it may alternately advance the fangs and refold them once or twice.

The mechanism whereby a snake can breathe, even though its mouth and throat be crowded with a large animal, is provided by the structure of the trachea or windpipe. This opens near the anterior tip of the lower jaw and is not collapsible. The glottis (the outer end of the trachea) is not fixed in position; it may be caused to extend out into the air below the prey to serve as an air intake while the swallowing proceeds.

#### LICKING PREY

It was once a common belief that rattlesnakes, before eating prey, lick it all over, covering it with slime to facilitate the swallowing process (Beverly, 1722, p. 65; Kalm, 1752–53, p. 60; Byrd, 1929, p. 158 [written in 1728]; Wesley, 1770, vol. 1, p. 173; 1784, vol. 2, p. 35; Lombard, 1881, p. 88). This myth is still heard today (Bealer, 1921, p. 69). An examination of a rattlesnake's tongue will show the impossibility of such an idea; for so thin and delicate an organ, even if it dripped saliva, would require hours to cover the smallest mouse. The explanation of this widespread idea is simple: Someone comes upon a snake that for some reason has regurgitated its prey, heavily coated with saliva and digestive juices as it would be, and jumps to the conclusion that it had been coated before being swallowed.

As an example of this unsound reasoning, W. (1846, p. 62) saw a rattler swallowing a small ground squirrel. When the snake had the rodent partly down it became frightened and regurgitated. It then, according to W., covered it with slime and reswallowed it. What really happened was that the prey became covered with the slime while it was being partly or entirely swallowed the first time.

#### DISGORGING PREY

Rattlesnakes have no difficulty in disgorging prey that has been completely swallowed, as anyone knows who has taken the trouble to force-feed a snake, only to have the food shot out in a fraction of the time it took laboriously to work it in. But during the course of the swallowing process a rattler may sometimes have difficulty in getting rid of the food. For example, Grinnell and Grinnell (1907, p. 53; Grinnell, 1908, p. 169) found a small southern Pacific rattlesnake with its mouth so completely gagged by a half-swallowed meadow mouse that it was unable to rid itself of the prey and therefore could be handled quite safely. Bogert (1927, p. 298) recounts a similar case of a Mojave rattlesnake found while engaged in swallowing a kangaroo rat. Although the snake was infuriated, it seemed unable to throw up the rat so that it might pay its respects to the intruder. Woodbury (1933, p. 8) found a young Great Basin rattler eating a Woodhouse jay. When the snake tried to disgorge the bird, its bill caught in the snake's throat and actually punctured the skin. One of my correspondents also mentions such an experience:

Rattlesnakes do not seem to be able to disgorge anything they have started to swallow. I killed one eating a young rabbit and he couldn't or wouldn't let loose of it. *Lawrence Kelly, Harper, Oreg.*

But difficulty in rejecting prey is not always evident during the swallowing process. McLean (1926, p. 62; see also Van Duyn, 1943, p. 63) found a northern Pacific rattler swallowing a golden-mantled ground squirrel, with only the hind legs and tail of the prey protruding from the snake's mouth. When poked, the snake disgorged its prey immediately. The fact that the squirrel was so large as to tax the snake's swallowing capacity was indicated by the almost useless condition of the lower jaw for some time after the prey had been regurgitated. Three of my correspondents report somewhat similar experiences:

Contrary to common belief that rattlers cannot disgorge half-swallowed objects, I have seen them, when teased, disgorge squirrels that were more than half swallowed. If left to themselves they will go back and continue their meal. *H. Lee Morris, U. S. Fish and Wildlife Service, Tulelake, Calif.*



I once killed a big southern Pacific rattlesnake in the Angeles National Forest. He had killed and partly swallowed a brush rabbit,<sup>17</sup> head first. When struck with a rake, and slightly injured, he quickly spit out the rabbit and coiled. I thought this interesting, as I had believed a rattler in the act of swallowing his prey was helpless to defend himself for some little time. *T. B. Niehaus, U. S. Forest Service, Challenge, Calif.*



I observed a rattlesnake eating a ground squirrel, *Citellus* ssp. It was about one-half in the snake's mouth, and was being swallowed head first. It was immediately and easily disgorged when I approached. *Don S. Simpson, Deputy Game Warden, Saratoga, Wyo.*

When an animal has been completely swallowed there never seems to be any difficulty in throwing it up. Rattlers are easily frightened and will disgorge their

<sup>17</sup> *Sylvilagus bachmani cinerascens*.

food if handled after a meal, a habit well known to all zoo custodians (see also Gamble, 1934, p. 230). Occasionally a rattler, disturbed while feeding, may manifest a greater irritability than is normal. Kalm (1752-53, p. 315) expressed the opinion that rattlesnakes are more irritable when hungry. However, this might well be interpreted as indicating alertness rather than anger. Pierce (1933, p. 62) came upon a southern Pacific rattlesnake as it was eating a young mountain quail. The snake, prevented from escaping, disgorged the bird and went for the intruder.

I found a rattlesnake eating young jackrabbits. I watched him swallow one, and when he took hold of a second I stepped in. The snake began to rattle even before he saw me, and became very mad. He released the rabbit and coiled by a bush, ready to strike. *Robert M. Parkhurst, U. S. Fish and Wildlife Service, Weiser, Idaho.*

#### DEAD FOOD

Under the conditions of captivity, rattlesnakes eat dead creatures quite readily, and it is known that they occasionally do so in the wild.

Once I surprised a large rattler getting ready to swallow a ground squirrel that had been dead for some time, as the carcass was badly swollen. *M. D. Morris, U. S. Forest Service, Pollock Pines, Calif.*

Kolb (1946, p. 22) tells of shooting a squirrel out of a tree. He then went after two others; when he returned to the first it was being swallowed by a large "coon-tailed" rattler (western diamond, *C. atrox*). In this instance the squirrel may not have been dead when the rattler found it beneath the tree. LeRay (1930, p. 203) reported finding a massasauga (*S. c. catenatus*) that was eating a frog, the legs of which were so stiff he judged it must have been found dead. Swanson (1952, p. 181) observed two instances in which timber rattlers (*C. h. horridus*) had eaten dead prey.

In another case, a southwestern speckled rattlesnake (*C. m. pyrrhus*) ate a ground squirrel that had been shot and left in a field some three hours before. At 7:30 in the evening of May 23, 1946, C. B. Perkins and I came upon a sidewinder (*C. c. laterorepens*) that was swallowing a dead kangaroo rat (*Dipodomys*). The rat was moderately stiff, and a cut on one side showed that it had been a traffic casualty.

It is not at all unusual to find rattlesnakes attempting to eat mammals that have been caught in traps. F. F. Gander, following up a trap line, found a red diamond rattler (*C. r. ruber*) that was swallowing a trapped rat, and was making every effort to get past the obstruction of the wire spring. Wade Fox told me of finding a speckled rattler (*C. m. pyrrhus*) nosing a *Peromyscus* caught in one of his traps. Von Bloeker (1942, p. 38) reported a southern Pacific rattlesnake that was trying to swallow a trapped silky-haired pocket mouse.

#### FATAL MEALS

Occasionally one hears of a meal that has proved fatal, the rattlesnake being unable either to engulf the prey or rid itself of the half-swallowed encumbrance:

About two years ago I found a dead rattlesnake which had about half-swallowed a young cottontail, and it had evidently choked the snake to death. I could find no other sign of injury on the snake. *A. L. Alexander, U. S. Forest Service, Roosevelt, Ariz.*



On one occasion I found a rattler dead with a bird in its mouth. Evidently the snake had attempted to swallow the bird and it got caught in its mouth, and the snake finally died. *W. T. Sweet, Butte, Mont.*

Fitch (1949a, p. 552) tells of a small, rather emaciated young northern Pacific rattler that was kept with several others in a pit where natural conditions were simulated. One night it ate a pocket mouse, and on the following morning its movements were so handicapped by the large meal that it was unable to reach its accustomed shelter and was killed by the sun. Quelch (1891, p. 9) tells of a young South American rattler (*C. d. terrificus*) that died while trying to swallow a harmless snake longer than itself.

Horned toads are occasionally fatal to rattlesnakes, as they are to other snakes as well. A horned toad held by the head, will swing it from side to side, as if deliberately seeking to cause injury with the horns. Van Denburgh (1922, vol. 2, p. 957) reported a sidewinder found with a desert horned toad (*Phrynosoma p. platyrhinos*) partly swallowed. The horns had penetrated and protruded from the lower surface of the snake's neck. Vorhies (1932, p. 372; 1948, p. 303) shows a picture of a small Mojave rattlesnake (*C. s. scutulatus*) found with a regal horned toad (*P. solare*) that it had tried to swallow. The horns had pierced the snake's throat and neck. The snake was still alive when found, but died soon after. Milne and Milne (1948, p. 27; 1950, p. 725) state that the skeletons of rattlers that have tried to swallow Texas horned toads (*P. cornutum*) have been found in Texas. But Bogert noted a captive sidewinder (*C. c. laterorepens*) that ate a Texas horned toad without suffering injury. Short-horned horned toads (*P. douglassi* ssp.) have horns that are too short and dull to cause inconvenience to a rattler. Instances of their being eaten have been reported under the food habits of *C. v. viridis*.

Erickson (1950, p. 43) found a live timber rattler that had several porcupine quills protruding from its jaw. Evidently it had struck a porcupine. Watson (1754, p. 289) states that when a rattler eats a white hedgehog, the skin is digested and the rattler is killed by the loose prickles. As hedgehogs are Old World creatures, inaccessible to rattlesnakes, the story may have reference to porcupines.

In the *Pennsylvania Game News*, vol. 25, no. 11, p. 38, November, 1954, there is a note concerning a timber rattler (*C. h. horridus*) that was found with a dead squirrel in its mouth. The squirrel had its teeth so locked on a part of the rattler that it could neither be swallowed nor ejected. When found, the snake was rattling and writhing. Presumably it would have died from this posthumous revenge of its victim.

#### REACTIONS OF PREY

While the fascination of birds and mammals by rattlesnakes is no longer believed possible by those who have given the closest study to the habits of the snakes, other reactions upon the part of animals that normally serve as the food of snakes are well authenticated. Grinnell and Grinnell (1907, p. 53) located three snakes by following the excited calls of a number of birds in a rose thicket. It is not unusual to find birds chattering noisily about a snake. A. M. Jackley located prairie rattlesnakes by observing a characteristic neck-craning by meadow larks. The actions of turkeys, which, upon finding a snake in a field, circle around it with warning cries, are well known. This reaction has even been used to aid in the collection of snakes (H. M. Smith, 1946, p. 63).

Of the studies thus far made on the reaction of mammals to rattlesnakes, those on the California ground squirrel (*Citellus beecheyi*) have been the most com-

plete. Linsdale (1946, p. 67), Fitch and Twining (1946, p. 66), Fitch and Glading (1947, p. 104), and Fitch (1948a, p. 554) have presented the results of extensive field observations. Linsdale, in his detailed notes, has thus described the typical ground-squirrel reaction:

The responses of ground squirrels to rattlesnakes are especially striking. The behavior of a squirrel in the presence of a snake is recognizable and we have not seen it demonstrated under any other circumstances. The ground squirrel uses its tail for a special kind of communication. The squirrel approaches within a foot or two of the snake, its tail held nearly vertical and thrashed from side to side three or four times at intervals of a few seconds. It faces the snake, occasionally taking a few stiff steps toward or away from it, and may keep this up for three minutes or longer, seeming reluctant to turn its back toward the snake. Other squirrels may approach, starting to wigwag their tails when about 10 feet off, sometimes seeming to wigwag as the leader did, and directly after, as if transmitting a signal. The raised tail and the wagging are kept up for half a minute or longer after leaving the vicinity of the snake. The snake may be in the grass or in a burrow. This type of behavior is strictly limited to the presence of rattlesnakes, but it is an established procedure. It has been reported for other localities and the similarity of the performance is impressive. At the same time much variety is expressed because the circumstances of each encounter differ.

Dr. Linsdale also noted that young ground squirrels, upon issuing from a burrow that harbored a rattlesnake, although they were otherwise uninjured, rubbed their eyes as if affected by something objectionable. This reaction should have further study. Linsdale's observations were made at the Frances Simes Hastings Natural History Reservation, Monterey County, California. The only rattlesnake occurring there is the northern Pacific rattler (*C. v. oregonus*).

Dr. Joseph S. Dixon, field naturalist of the U. S. Fish and Wildlife Service, wrote me of a ground squirrel that walled itself off from a rattler:

At Miguel Meadow in Yosemite National Park on July 7, 1940, we found at 3 P.M. a large Pacific rattlesnake resting halfway down a California ground squirrel burrow. Just 74 inches away an excited adult ground squirrel poked its head out of another burrow, seemingly connected with the burrow the rattlesnake was in. One of the students approached to within eight feet of the snake and as soon as the man's shadow fell on the snake it turned and fled down into the squirrel burrow. We saw the adult ground squirrel run down the other burrow and soon heard it digging furiously, evidently in an attempt to wall off and plug its burrow so the rattlesnake could not reach it.

While the students stood guard I took a shovel and dug out both burrows, and found a dirt plug between the squirrel and the snake.

Osborn and Allan (1949, p. 330) watched several young prairie dogs approach their holes with a peculiar stiff-legged gait. Some went down a hole, immediately reappeared, and then entered another. The authors investigated and heard a rattler rattling in one hole. Pequegnat (1945, p. 89) found evidence that a kangaroo rat had kicked dust at a rattlesnake three times.

Whether rattlesnakes ever use any means of luring prey within striking distance is not known. One of the early theories of the purpose of the rattle was its use in the attraction of birds by imitation of such insects as the cicada. This theory is no longer given serious consideration. But A. M. Jackley thought the rattle might bring some creatures within range through curiosity. He wrote:

The first reaction of a rattlesnake, when a bird lands close by, out of curiosity, is to rattle. This is true also if a chipmunk approaches. When the snake rattles the bird will take

flight, or the chipmunk will run away a short distance. They are frightened by the rattle, but soon return with their curiosity more thoroughly aroused. That the rattling does intensify the curiosity of the prey is apparent. One need only to observe fowls such as chickens and turkeys to determine that. I have witnessed so many instances in which the snake was approached by a curious horned lark or meadow lark, and their reactions were so plain, that I have no doubt concerning this effect of the rattle.

Kauffeld (1943b, p. 612) noted that young banded rock rattlesnakes (*C. l. klauberi*), which have bright yellow tails, wave them with a more or less regular motion while the snakes are otherwise quiet. He thought this might be in imitation of grubs for the purpose of luring the lizards upon which these young snakes feed, but did not succeed in proving that this was the purpose of the peculiar action. Juvenile southern Pacific rattlers (*C. v. helleri*) also have bright yellow tails, which color changes to gray or black as the snakes age. But they have not been observed to indulge in tail-waving as did the young *klauberi*. Allen (1949b, p. 225) noted that juvenile Mexican moccasins (*Agkistrodon b. bilineatus*) waved their conspicuously yellow tails to attract frogs. The tails were actually snapped at by the frogs, which, in turn, were seized by the snakes. A further discussion of tail-waving is that of Burger and Smith (1950, p. 431).

#### INTERRELATIONSHIPS OF RATTLESNAKES AND PREY

That food availability greatly affects the ranges and habits of all rattlesnakes, goes without saying. Kauffeld (1943b, p. 610) has called attention to the fact that the young lizards, upon which the small species of rattlers (e.g., *pricei* and *klauberi*) feed, are born at the same time as the predators themselves, a condition favorable to snakes' survival. However, nearly all reptiles in the southern part of the United States are born or hatched in the early fall, whether prey, predators, or without interrelation. I have myself tried to ascertain whether rattlesnakes are more plentiful on the roads at night when rats and mice are also particularly numerous, but I am still not sure that there is any correlation. Mammals are much less dependent for their activity on suitable air and ground temperatures than the rattlers, so that they were sometimes abundant on nights when the snakes kept to their holes. But it is true that on certain occasions when the mammals seemed particularly numerous, the snakes were also plentiful (Klauber, 1939a, pp. 18, 29).

Fitch (1949a, p. 547; see also Howard, 1953, p. 431) has discussed various seasonal and other relationships of the northern Pacific rattlesnakes and their prey on the San Joaquin Experimental Range. Here the rattlesnake is the most abundant of the predators, with a population that he estimates at 1.19 snakes per acre. They eliminate one or two ground squirrels per acre per year (1948a, p. 593). Fitch calculates that the rattlesnakes and gopher snakes (*Pituophis c. catenifer*) together account for the destruction of 37 per cent of the annual ground-squirrel increase (34½ per cent by rattlers), but much less of the other rodents that they eat. He also points out (1949a, p. 549) how favorably the seasonal activities of the ground squirrels fit with those of the rattlers from the standpoint of the latter. The ground squirrels are diurnal. The young are born in the spring and are about a third- to half-grown at the time when the rattlers are diurnal and most active. Not only are young ground squirrels of just the proper size to furnish a full meal for an average adult snake—only an exceptionally large male rattler could swallow a full-sized

ground squirrel—but the young, in their incautious gambols, are more likely to come within range of a waiting snake. Later, when the squirrels have grown too large and the snakes have been relegated to night forays by the diurnal heat, the nocturnal kangaroo rats bear the brunt of predation.

## FOOD REQUIREMENTS

### FREQUENCY OF FEEDING

Studies of captive specimens indicate that mature rattlesnakes thrive on an adequate meal every 14 to 18 days. In the wild it may be supposed that the energy consumed in hunting for food and similar activities leads to a slightly greater intake requirement; necessarily the meals secured would be more irregular with respect to both frequency and size. Young rattlers, with a greater need for food during their stage of rapid growth, feed more often than adults, if they can find suitable prey.

Most of the statements regarding the frequency with which rattlers eat in the wild have been mere guesses. They have varied from every two days (Rolker, 1905, p. 204) to three times per year (Stillwell, 1939, p. 17). But recent field studies of the stomach contents of large series of rattlesnakes are beginning to give us data that, co-ordinated with observations on captive snakes, permit more reliable conclusions.

Fitch and Twining (1946, p. 64) made surveys of the food habits of the northern Pacific rattlesnake (*C. v. oreganus*) at the San Joaquin Experimental Range in California. One of their lines of research was to determine the proportion of the snakes that contained the remains of food. Their report says (p. 68):

Stomach contents were dissected from dead snakes and palpated from live ones. Undoubtedly in the live snakes many well-digested prey items that might have been revealed by dissection were overlooked because too much digested to be forced up by manipulation. Hence the ratio of snakes containing food was low—only 79 of the total number of 521.

They give the following monthly distributions of the ratios of the snakes containing food to the total examined: March: 3 out of 36; April: 22 out of 123; May: 26 out of 140; June: 14 out of 88; July: 10 out of 31; August: 2 out of 41; September: 0 out of 34; October: 1 out of 21; November: 1 out of 7; total: 79 out of 521, or 15.2 per cent. These figures show that the highest proportions of snakes containing food occur in the months of April to July, but the highest single month (July) was only 32 per cent. Fitch (1949a, p. 549) gives a later figure of 164 out of 1,128 containing food in the stomach, or 14.5 per cent.

Uhler, Cottam, and Clarke (1939, p. 607), who made complete dissections of their snakes, not turning them loose for further study as did Fitch and Twining, found recognizable food in 141 out of 253 timber rattlers, or 56 per cent. This indicates, as expected, that examinations of live snakes do not disclose the complete contents of digestive tracts. If it be assumed from the Uhler, Cottam, and Clarke data that half of the rattlesnakes contain at least some remnants of food in the intestinal tract, and that complete elimination requires 5 to 8 days—as seems to be indicated by studies of the digestive processes of captive snakes—we reach the conclusion

that adult rattlesnakes feed every 10 to 16 days. It is my belief—again based in part on observations of captive specimens, which do well when fed at intervals of two to three weeks—that this approximates actuality, at least at times of major activity. Of course, at best, this estimate of the intervals between feedings is only an average figure—one subject to wide variations as affected by the season, the temperature, and the fortunes of the chase.

As to seasons, it is believed that rattlers are especially active in pursuit of food, first, in the spring to replenish the fat consumed during the long period of hibernation; and, second, in the fall to restore any fat depleted by inactivity during summer, in order to be prepared for the next winter's complete seclusion. However, it is essential, when the food is secured in the latter season, that there be sufficient warm weather to insure digestion before the onset of the cold stops this vital process. These seasonal differences are necessarily dependent on temperatures and therefore on both latitude and altitude.

Fitch (1949a, p. 550) believes that the adult northern Pacific rattlesnakes on the San Joaquin Range annually require twice their weight in food in order to keep in good condition. This would involve only six meals of ordinary size during the active season of seven months, for an average meal is equal to from 30 to 40 per cent of the snake's body weight. This is a larger intake per meal than is contemplated in the figure I have given of a meal every 10 to 16 days during the active season. As I have said, my estimates are based in part on captive snakes at the zoo, and here a normal meal for an adult rattlesnake is about 25 per cent of its weight. There are sexual differences as well; the females, heavy with young in midsummer, are even more restricted than the males to hunting in the spring and fall.

Temperatures, whether seasonal or diurnal, are of great importance in the feeding schedules of snakes. First, they affect the metabolic rate and hence both the food requirements and the rate of digestion; and, secondly, they control muscular activity and hence the ability to hunt successfully. These two effects are obviously interrelated. There are upper limiting conditions as well; and at both extremes they work together rather than in opposition. Below the optimum temperature the snake needs less food, and has less ability to secure it; above the optimum he will be driven below ground by temperatures he cannot withstand, but is fortunate in that his refuge—some mammal hole or rock crevice—may also be the refuge of his prey, to the latter's undoing.

Since snakes are more seriously affected by temperatures—either high or low—than are birds or mammals, and cannot remain active under extremes that the higher vertebrates can easily withstand, it is to be expected that they will seek to improve their lot by hunting prey during that part of the day or night when the temperature is most to their liking. This they do, but at the same time their hunting must be arranged to coincide with the activities of the prey. Since mammals comprise the bulk of rattlesnake food, it is to the advantage of the snakes that rodents are also largely nocturnal or at least crepuscular.

The actual temperature limits for the snakes lie between about 60° and 100° F.; that is, the air and ground temperatures together with the solar radiation must be such as will result in body temperatures within these limits. This range, in fact, includes exceptional conditions; it is probable that feeding generally takes place at body temperatures between 70° and 90° F., with an optimum centering at about 83° F.

Nocturnal activity, if a rattlesnake be driven to it by temperature, is not a handicap. Not only are some of its principal food sources nocturnal, but it has a special sense, independent of light, and in fact aided by darkness and low temperatures, for prey detection. This is provided by a special sensory organ—the facial pit—for the location of warm-blooded prey; and as rattlers depend upon this and an acute sense of smell, more than upon sight, they are well equipped to hunt at night, when small mammals, such as rats and mice, are particularly active. However, in the spring before the onset of diurnal temperatures above the rattlesnake's endurance, the snake is fortunate in that this is the season of prevalence of young ground squirrels and cottontails, which may best be hunted in daytime.

That chance in securing prey must entail wide discrepancies in the intervals between meals is so evident that it requires no discussion. A snake that finds a small creature will be satisfied only for a few days and then must search for another; or it may continue to hunt until it has eaten a bulk equal to a full meal. Should a rattler be fortunate in finding a single animal equal to its capacity, there will no doubt follow a maximum interval between feedings consistent with the seasonal food requirement.

Summarizing these effects of seasons, temperatures, bodily requirements, and the availability of prey, I should express the opinion that adult rattlers of the larger species require a full meal every 10 days to 2 weeks in the spring, every 3 weeks in the summer, and every 2 weeks in the fall, with the total meals per annum dependent on the length of the active season.

It is only natural that one should ask why a rattlesnake's schedule of meals is so completely at variance with what we should ordinarily expect from a knowledge of other animals. This results from several different, but interrelated, phases of a single general condition—the reptile's almost complete lack of internal temperature control, as discussed elsewhere (p. 411). A bird or mammal fixes and maintains a constant or nearly constant internal temperature—that best suited to its own life processes. This level is maintained by internal heating through oxidation of the carbohydrates secured from food when a rise in temperature above the surroundings is necessary; and by cooling, usually through evaporation of water from the lungs or skin, when a high temperature of the surroundings tends to raise the body above the optimum. The maintenance of a fixed optimum body temperature is favorable to the life processes, including muscular activity and food digestion; but this maintenance is at the expense of energy contained in the food when the exterior temperature is below the optimum, as is nearly always the case, or at the expense of water when above.

The snake, an ectothermic animal lacking this control, is at the mercy of wind and weather, for its temperature is that produced by its surroundings, particularly of the ground upon which it rests and the air, and by the solar radiation impinging on its body. It can exert muscular activity and digest food only when these external factors maintain a body temperature within a certain range. But, coincidentally, the lack of a temperature differential between its body and the surroundings results in little heat loss by radiation or convection; its digestion is geared to a lower temperature and is slower than that of birds and mammals, for otherwise it could eat only in midsummer; and its muscular activity is less. All of these factors lead to a lower food intake requirement than that of warm-blooded, or endothermic,

creatures. As an indication of the relative food requirements of ectothermic and endothermic animals, C. J. Martin (1930, p. 561) has stated that, per unit of surface, and for bare existence at 15° to 20° C. (59° to 68° F.), a lizard requires only 2½ per cent of the food required by a man. See p. 412 for explanations of the terms ectothermic and endothermic.

One other condition tends to stretch the average time between feedings. The snake's extensible jaws, and the physiology of its intestinal tract, permit the ingesting of food items that are relatively large compared with the bulk of the snake. Fitch and Twining (1946, p. 69) found that the prey of northern Pacific rattlesnakes averaged 40 per cent of the weight of the captor, the range being from 3½ to 123 per cent. Fitch (1949a, p. 550) later concluded that two-fifths of the body weight would be an average adult meal. At the San Diego Zoo we have observed that a rat equal to one-fourth of the snake's weight constitutes a satisfying meal, but one that cannot be considered large as measured by its full swallowing capacity. But these ratios of meal to body weight are all relatively larger than the ratios represented by the meals of warm-blooded carnivores.

Fitch (1949a, p. 571) has calculated the differences in the food requirements of rattlesnakes as compared with certain warm-blooded predators. He estimates that an adult rattlesnake—although weighing one-fifth as much as a red-tailed hawk—annually eats only as much as would satisfy a hawk for a few days; and a rattlesnake's yearly requirement would furnish but a single meal for a coyote. More frequent feeding is the penalty the warm-blooded creatures pay for their higher metabolic requirements and reduced capacity per meal.

Both the vicissitudes of the rattlesnake's method of securing prey, and the necessity for a long hibernation in most climates, render a considerable fat storage necessary for survival. Benedict (1932, p. 408) states that nearly all cold-blooded vertebrates are plentifully supplied with such storage. This allows the snake to survive irregularities in the feeding period that may multiply, by many times, the intervals we have assumed to be normal. In fact, it is not unusual, as I shall mention later, for captive rattlers to live over a year without food. Pollard and Young (1952, p. 134) mention the lobes of fat deposited in rattlesnakes along both sides of the intestines from the stomach to the vent. This is nearly or completely exhausted at the end of the period of hibernation. (It is from this fat that rattlesnake oil is secured.)

Fitch and Twining (1946, p. 69), from their experiences on the San Joaquin Experimental Range, have this to say concerning the food requirements of young snakes:

Conditions favoring a high population of rattlesnakes probably could exist only in a habitat affording an abundance of several different prey species, which would provide adequate food sources for snakes of every size. Abundance of small rodents and lizards favors successful development of the smaller snakes. The area of the Experimental Range has relatively high populations of rats and squirrel-sized rodents, providing a food source for the larger snakes. But, compared with many other areas in the western states, its populations of lizards and mouse-sized rodents are low. Though several species are present, none is particularly abundant, and all are subject to marked fluctuations in numbers. Thus small rattlesnakes on this area are less well supplied with food than are adults, and a critical stage in the life cycle may occur during the first few months of life. During the late summer many young have been found in emaciated condition and we suspect that a high proportion of each season's brood dies before reaching the age of a year, partly through lack of sufficient food.

That the high mortality among the juveniles is in part due to an inadequate food supply cannot be doubted, but this may be secondary, although related to, the inroads of predators. We have noted in captive broods at the San Diego Zoo that those individuals that accept food quickly outstrip their brothers in growth. In the wild, failure to get food readily would seriously affect the chances of survival in two ways: First, there is the weakness inherent in lack of food, for the young rattler, needing all his nourishment for growth, is without fat storage and therefore must have his meals more often and more regularly than adults; and, secondly, failure to secure prey keeps him in the open hunting for it at the particular stage of life when he is subject to many predators that could neither cope with, nor eat, an adult rattler. Another disadvantage suffered by the young rattlers is their greater dependence on lizards, which are largely diurnal, a further temptation to dangerous daylight forays.

Food habits no doubt affect the young of some rattlesnake species differently than others. In western San Diego County, adult southern Pacific rattlesnakes (*C. v. helleri*) and the red diamonds (*C. r. ruber*) are equally common. There seems to be no difference in either their seasonal or diurnal periods of activity. Yet there are probably 10 juvenile southern Pacifics observed to every young red diamond. This may be, in part, because the red diamonds, which are slightly larger, are less dependent on lizard prey, but this cannot be the only reason for so marked a difference in their apparent numbers.

It is no doubt significant that the smaller species of rattlers, such as *miliarius*, *lepidus*, *pricei*, and *cerastes*, are found in areas where mouse-sized mammals, or lizards, or both, are abundant. However, I do not intend to imply that this is a simple case of sole cause and effect by which the ability of small species to survive is determined; temperature-mass considerations affecting heat absorption and dissipation are also important in delimiting the climates in which animals can live.

With regard to post-natal growth, Trouslot (1887, p. 86) reported that young massasaugas grew three or four inches without either food or water, but this is doubtful. Wright (1941, p. 667) agrees that lack of food is an important source of the high mortality among juveniles, although the young are able to live for a while on the remaining contents of the yolk sac. He states that the yolk sacs are drawn into the body shortly after birth, which is contrary to our observations; for, in all the normal births we have witnessed at San Diego, the young were born with the yolk sacs already absorbed, as was evident from their distended bellies. Allen (1933, p. 14) had occasion to dissect two female black-tailed rattlers, one of which contained young in a more advanced stage of development than the other. In the less-developed young, the yolk sacs were still external, while in the brood nearer birth the sacs had already been enclosed within the body.

We occasionally find, in the wild in the late spring, young rattlesnakes but little larger than the normal size at birth in autumn. It is probable that these are not the result of off-season births, but, rather, are snakes born at the usual time in the fall that have been unsuccessful in obtaining adequate food, yet have managed somehow to survive.

## EFFECT OF SHEDDING

Skin-shedding, as shown by observations of captive rattlesnakes, does not seriously affect their hunting for prey, except for a few days two to four times a year. Although some captive specimens will take food when in the first stages of shedding—the “blue-eyed” stage when sight is interfered with by the partial opacity of the eye covering—it is to be doubted that wild specimens would hunt during such a period. Although rattlesnakes are probably more dependent on olfaction and the facial pit than on sight to secure prey, they no doubt seek concealment when deprived of the protection of the rather poor eyesight that they do possess.

## MULTIPLE MEALS

From what has been said it will be evident that we are still none too sure of the frequency with which rattlers feed in the wild. But we do know that they are successful in engulfing prey that seems quite beyond the distensive capacity of their jaws and neck—an attribute shared with all snakes—and that the stomach contents often include several different creatures, thus showing they have not been surfeited by the first animal secured.

I have already described the jaw mechanism by which rattlesnakes are enabled to swallow such relatively large creatures, and this without the help of teeth that can chew or tear, or hands or feet to hold or manipulate. Full-grown cottontails and even young jackrabbits are not beyond the capacity of the largest rattlesnakes, such as the diamondbacks, and those of more moderate size feed on mammals as large as squirrels and prairie dogs. Even the juveniles are frequently found to contain mice of a surprising bulk. For example, Bryant (1925, p. 72) noted that a rattler only two feet long and an inch in diameter had swallowed a wood rat nine inches long (not including the tail) and two and a half inches in diameter. Rodgers and Jellison (1924, p. 12) observed that a prairie rattler weighing 414 grams had swallowed a ground squirrel weighing 297 grams. Such huge meals are not exceptional. Fitch and Twining (1946, p. 69) record an instance in which the prey actually exceeded the weight of the rattler that swallowed it by as much as 23 per cent.

While the taking of a single animal of large size would no doubt satisfy a snake for two weeks or even more, the presence of several items of prey in the digestive tracts of a number of specimens shows that swallowing two or three creatures of more moderate size is quite usual. Sometimes these are taken at a single time and place, as happens when a rattler finds a litter of young rabbits or a nest of birds, but more frequently they are diverse creatures, evidence that the snake continued hunting after securing the first animal.

That a rattler will clean out a nest, or at least feed to repletion, when it comes upon a litter of young mammals or a nest of birds, is evident from a number of reports. I have myself noted from two to four young cottontails in a snake. Fitch (1949a, p. 549) mentions litters of three and four that had been eaten. Atsatt (1913, p. 44) killed a southern Pacific rattler that contained four young ground squirrels.

Three of my correspondents, all from Wyoming, report having found prairie rattlers (*C. v. viridis*) that were eating young meadow larks in a nest; they had eaten three, four, and five birds, respectively. Keep (1882, p. 27) shot a canebrake rattler (*C. h. atricaudatus*) that had several young quail in the stomach. Nauman

(1929, p. 331) found a timber rattler (*C. h. horridus*) in eastern Iowa that had eaten an adult field sparrow, together with its brood of nestlings.

Domestic creatures sometimes fall victims. B., J. (1765, p. 513) tells of a rattler that had eaten 15 young turkeys in a brood. A newspaper report appeared July 11, 1937, concerning a farmer at Jamestown, Tuolumne County, California, who found, in one of his rabbit hutches, a northern Pacific rattlesnake that had eaten a litter of 10 young rabbits.

Several of my correspondents tell of experiences to the effect that a rattlesnake, coming upon several birds or mammals, may strike and kill a number before starting to eat one:

They are wanton killers; for instance, my wife had some pound-size chickens in a coop. She heard a commotion and ran out. A four-foot rattler had killed three, and she saw him strike a fourth. It lived about half a minute after it was bitten. *J. W. Crigger, U. S. Forest Service, Huntersville, W. Va.*



I had a hen and some small chicks in my poultry yard. When the hen made a noise, my wife went out to see what was causing the trouble. A small timber rattler had killed three of the chicks and was swallowing one of them. *J. L. Huggins, Game Warden, Mullins, S. C.*

But most of the stomach contents of rattlesnakes containing several food items indicate that they were secured at different times—that the snake, not satisfied with the first animal, continued to hunt for more, sometimes immediately after the first was eaten, sometimes later, but at least before digestion of the first was complete. Grinnell (1908, p. 170) found a southern Pacific rattlesnake with two chipmunks in its stomach. The more complete dissolution of the first one swallowed indicated that there may have been an interval between their capture. Out of 164 northern Pacific rattlesnakes that Fitch (1949a, p. 549) found with food in their stomachs, or with freshly killed prey, only six had more than a single food item. Two had young cottontails, secured in a nest; two had each eaten two ground squirrels; one contained a fence lizard and a pocket mouse; while the last had eaten two adult meadow mice. But the study of scats (Fitch and Twining, 1941, p. 71) suggests a larger percentage of multiple meals, for there were 10 out of 90 that included the remains of two different animals. While the components may have been taken some time apart, it is at least evident that the second was secured before the remains of the first were completely eliminated.

Tevis (1943, p. 243), after watching a red diamond rattler strike and eat a young ground squirrel, saw it continue to hunt for more. On the following morning its swollen condition indicated that it had cleaned out a whole colony of young squirrels. Even so, when a young kangaroo rat was thrown toward its head, this was eaten as well. Linsdale (1946, p. 72) watched a northern Pacific rattler hunting for young ground squirrels, although already distended as if it had had a full meal. Fitch and Twining (1946, p. 67) found a rattler that seemed to have fed, yet was coiled beside a dying young ground squirrel as if preparing to enlarge its meal.

The following are some records of multiple meals that have appeared in print: Merriam (in Stejneger, 1893, p. 217) reported a sidewinder (*C. c. cerastes*) that had eaten a kangaroo rat (*Dipodomys*) and two pocket mice (*Perognathus*). Babcock (1929a, p. 13) shows an X ray of a timber rattlesnake (*C. h. horridus*) collected in Massachusetts that contained no less than seven small animals, including a shrew

and a meadow mouse. Hibbard (1936, p. 281) mentions another snake of the same subspecies that had swallowed two gray squirrels two-thirds grown. Anon. (1938a, p. 166) reported a western diamond (*C. atrox*) that had eaten a full-grown cottontail and a quail. Von Bloeker (1942, p. 38) reported a particularly surprising assortment of food in the stomach of a southern Pacific rattlesnake, which, at the time was trying to swallow a silky-haired pocket mouse caught in a trap. According to Von Bloeker this snake had already eaten three Jerusalem crickets, a California toad, a pocket gopher, a harvest mouse, and two meadow mice. The crickets may have been ingested first by the toad, instead of having been eaten directly by the rattler.

My own correspondents have sent me several interesting records of multiple meals:

While skinning a large timber rattler which I killed on Cumberland Mountain last summer, out of curiosity I examined the contents of its stomach and found them to consist of a toad, part of a lizard, and part of some variety of snake, the remaining skin having an indistinct yellow stripe. I took it to be a garter snake. *R. J. McCormack, Tennessee Department of Conservation, South Pittsburg, Tenn.*



In eastern Oregon we killed as many as 21 rattlesnakes in one day in an alfalfa field, when hauling hay which was in the shock. I can remember one rattlesnake that was cut in two by the mowing machine that had 12 pocket gophers<sup>15</sup> in its stomach. *L. J. Cooper, U. S. Forest Service, Merlin, Oreg.*



I skinned one big Pacific rattler on Cortina Creek that contained two ground squirrels and a hen quail, the digestion of which had not begun. *R. M. Williams, Arbuckle, Calif.*

Other multiple meals mentioned by my correspondents have been these: three rats in one eastern diamondback (*C. adamanteus*); two rabbits in a timber rattler (*C. h. horridus*); two striped gophers in one prairie rattlesnake (*C. v. viridis*), and a small rabbit and a short-horned horned toad in another; a kangaroo rat (*Dipodomys*) and a whiptail lizard (*Cnemidophorus t. tigris*) in a Great Basin rattler (*C. v. lutosus*); several birds, one of which was a western mockingbird, in a southern Pacific rattler (*C. v. helleri*); and an antelope ground squirrel and a pocket mouse in a Panamint rattlesnake (*C. m. stephensi*). I have found more than one food item in specimens of *cerastes*, *laterorepens*, *horridus*, *pyrrhus*, *helleri*, and *viridis*. Mixed lizard and mammal remains were not uncommon.

#### DIGESTION

Some curious ideas about the digestive processes of snakes have been recorded from time to time. Kalm (1752-53, p. 69) thought that if a rattler ate something too large to swallow, it could hold the posterior part of the meal in its mouth until the swallowed half had been digested. This was probably a misinterpretation of early notes by Byrd (1929, p. 158, but first published in 1733) which indicated that the head of an animal swallowed head-first may be well digested while the posterior is still in the stomach relatively intact. This has since been confirmed by others.

Motl (1936, p. 6) expressed the opinion that rattlesnakes have no stomachs, the food merely staying in the body until decayed. Brookes (1763, vol. 3, p. 370) correctly denied that rattlesnakes vomit up the indigestible parts of their food, as

<sup>15</sup> These must have been juveniles.

previously stated by Tyson (1683, p. 32). This is a mythical idea currently attributed to the Gila monster. It is true to the extent of egg shells, which are vomited by some egg-eating snakes, after they have been drained of their contents; but this is not true of rattlesnakes, which, like most snakes, digest the shells.

There has been much uncertainty as to the rapidity with which digestion proceeds. Beverly, as early as 1722 (p. 264), found the hair already disappearing from a rabbit swallowed 18 hours before. A. E. Brown (1881b, p. 106) expressed the opinion that digestion requires several weeks. Vorhies (1936b, p. 104) gives a figure of two or three weeks; Stillwell (1939, p. 17) estimates the interval at five to six weeks. Most estimates are considerably shorter. Reichert (1930, p. 262) noted that the eastern diamond rattlesnake (*C. adamanteus*) defecated two to three days after eating. Wright (1941, p. 668) gives this interval as 41 hours in the case of one meal eaten by a massasauga (*S. c. catenatus*) and 56 hours in another. Kauffeld (1943b, p. 611) says that most captive snakes in his care voided feces twice per feeding, which conclusions were at variance with those of Storer and Wilson (1932, p. 172), who recorded less than one void per feeding. Kauffeld, observing captive broods of *klauberi* and *pricei*, noted that defecation usually took place on the second or third day after feeding, and again on the fifth.<sup>19</sup>

Our own observations at the San Diego Zoo do not verify the regularity suggested by Kauffeld; on the contrary we have found great individual differences in frequency and intervals. An adult Tortuga Island diamond rattler (*C. tortugensis*) was fed 15 times in the course of a year and only 8 of these meals were followed by excretion prior to the next meal, 2 or 3 weeks later. In the 8 instances of excretion, from 3 to 16 days elapsed, with an average of 9 days. On the other hand, a southwestern speckled rattler (*C. m. pyrrhus*), also an adult, which was fed 17 times in a year, excreted no less than 46 times; only once were there no feces prior to the next meal, and in 2 instances there were as many as 5. The average elapsed time to the first excretion was 4½ days; and, where there were two or more, the average between the first and last was 6½ days.

Blain and Campbell (1942, p. 229) in an excellent series of X rays of snakes digesting rats—the snakes were not rattlers—have shown in detail the progress in the disintegration and digestion of the prey and the formation of excreta. Digestion was complete in somewhat less than five days.

These chronological discrepancies are explained by Benedict (1932), in his extensive studies of the physiology of large reptiles, including snakes; for he has shown that the rapidity of the digestive process is so dependent on the temperature of the snake—and therefore of its surroundings and impinging radiation—that comparative data on the time involved are quite valueless without a knowledge of the temperature conditions. Says Benedict:

Digestive activity, unless one is studying primarily the digestive processes, should likewise be avoided in comparative studies with cold-blooded animals. With these animals digestive activity persists for a much longer time than it does with warm-blooded animals, depending entirely upon the temperature of the environment and the temperature of the animal itself (p. 405). . . . In our digestion experiments with the boas it was shown that the length of time required for digestion is determined in large part by the temperature of the environment (p. 410).

<sup>19</sup> A king snake, having eaten a rattler, voided after seven days had elapsed. The feces included the rattle; the snake had been swallowed head first. The temperature averaged about 73° F.

Riddle (1909, p. 447) has discussed seasonal variations in the metabolism of cold-blooded vertebrates, including the effects of hibernation. A reduced amount of proteolytic ferment is secreted during the fasting period (p. 454). Volsøe (1944, p. 12) has reported on the hibernation of the European viper. He considers fat storage (p. 52) to be of primary importance mechanically to round out the posterior part of the body cavity, rather than having the usually stated purpose of energy production during hibernation.

It is much less usual to find the remains of prey in a rattlesnake's stomach than in the form of feces at the posterior end of the intestinal tract. Fortunately for the determination of what constitutes the prey, mammal hair is almost unaffected, so that identification is not difficult to a mammalogist. Lizard scales are more deteriorated and therefore difficult to identify, unless there be but one or two species found in the rattler's habitat. Sometimes one cannot be sure whether or not scales are present in feces; this may affect the accuracy of some of the statistics of the relative frequency of mammal and reptile foods, particularly such as are based on scatological data. Feathers are recognizable as such, and the species of bird can sometimes be determined. Fraser (1936-37, p. 74) suggests tying a piece of red thread—which would be indigestible—to any item of prey to determine the exact time of its intake and excretion by a rattler in captivity.

The bones of the prey are completely absorbed. Teeth are often found, but these are frequently the rattler's own teeth, including, especially, the fangs. The latter are better protected from the digestive juices than other teeth, since both the exterior and the internal venom duct are sheathed with enamel, whereas ordinary teeth are attacked and disintegrated via the pulp cavity. It is possible that internal damage may occasionally be caused by the passage of the fangs; Uhler, Cottam, and Clarke (1939, p. 612) report finding, in a copperhead stomach, a fang that had pierced the wall and caused a severe irritation.

Netting (1932, p. 13) stated that the teeth of the mammal prey are dissolved but not the claws. I have not observed any claws in feces. Fitch and Twining (1946, p. 69), from their studies of scats, reported that rodent teeth crumble; feathers and the bills of birds are somewhat disintegrated but can be identified. Foreign material is often found, such as sand, gravel, and sticks. It is of interest to record that the rattles of a rattlesnake remain unaffected in king snake feces.

#### WATER REQUIREMENTS

In captivity, when water is available in their cages, most rattlesnakes drink occasionally, and no doubt they do also in the wild. It has been reported—particularly of the timber rattlesnakes (*C. h. horridus*)—that at times when it is dry in their usual rocky habitats they roam down into the lowlands seeking water. Rattlesnakes drink by putting their snouts under water, making no attempt to keep the nostrils out so they can breathe. As a rattlesnake drinks, a pulsating movement is evident, particularly at the angle of the jaw. The water is forced inward by the opening and closing of the lower jaw; however, the movement is slight, and it is necessary to have one's eye on a level with the snake's head in order to see that the mouth is actually opened when the snake is drinking. A thirsty rattlesnake was observed to drink steadily for three minutes.

Rattlers have also been seen to drink from wet surfaces—a way of getting moisture from dew practiced by some lizards.

A rattler often gets its water off the surface of a rock, from dew on leaves, or the raindrops. I have watched them sip the moisture from a wet board, sucking it in like a vacuum cleaner. *Marion E. Rose, Pateros, Wash.*

Bogert (1927, p. 298) noted that specimens from the Mojave Desert (the Mojave rattlesnake, *C. s. scutulatus*) would drink in captivity only when water was sprayed on them or the rocks in their cage. They sucked the water off the rocks and sometimes off their own backs. One drank in this way for 45 minutes. Hedeger (1950, p. 86) says that rattlers prefer to suck water from drops sprinkled on their own bodies. Reynolds (1952, p. 66) mentions a rattler (probably *horridus*) that licked the drops off a board. Kauffeld (1943b, p. 612), with cage-born broods of *klauberi* and *pricei*, observed that the latter, particularly, preferred to drink water trickling over rocks. I have watched *pricei* drink water caught in the depressions of lily pads, while the snake was swimming in a goldfish pond with water all about.

The importance of water to rattlesnakes has been a matter of some difference of opinion. Probably there are considerable differences between species, those accustomed to well-watered habitats having a greater need than the desert forms. No doubt a desert dweller, such as the sidewinder, encounters water only on rare occasions and therefore must be largely dependent on its prey for its moisture requirements. As far as captive snakes are concerned, much depends not only on the food supply, but on the temperature and humidity at which they are kept.

Mitchell (1860, p. 4; Smith, 1882, p. 672) found water necessary to the eastern diamondback (*C. adamanteus*) particularly in hot weather or when it was about to shed. Ingersoll (1883, p. 35) says that in dry seasons rattlers often look for water in dooryards and houses; while Benton (1945, p. 80) states that in Arizona they come to water holes in the evening to drink like kittens. It is more probable that they have found dooryards and water holes good hunting grounds for prey. Kalm (1752–53, p. 315) thought timber rattlers, when hungry, frequented the banks of brooks to catch the animals that came to drink.

Storer and Wilson (1932, p. 170), experimenting with northern Pacific rattlesnakes (*C. v. oreganus*) in captivity, reported that these snakes needed no water beyond that secured in their prey, even when subject to the high summer temperatures experienced at Davis, California. They estimated the annual liquid intake of the snakes at about equal to their body weights. They point out that water evaporation is not a part of a temperature-regulating mechanism in reptiles as it is in warm-blooded animals, thus making water less necessary to survival. However, although rattlesnakes can survive without water, their health and longevity in captivity are certainly improved if water is available when they wish to drink.

Not only do snakes require less water because of its nonuse, normally, for temperature regulation, and the reduced temperature differences between the animal and its environment, which results in reduced evaporation, but also because the snake has a special water-conserving mechanism in the process of eliminating body wastes, in that the urine of snakes is excreted in the form of uric acid, a white chalklike solid (Babcock, 1912, p. 161). Benedict (1932, pp. 114, 422) has concluded that in spite of this mechanism, some snakes, such as the pythons and other kinds

with which he worked, do excrete some liquid; and that they also lose moisture, not only via the lungs in respiration, but through the skin as well. He found (p. 122) that there is an increased evaporation of water during the shedding period, which may verify the prevalent idea that shedding snakes seek water. Volsøe (1944, p. 69) believes that the mechanism whereby the solids in the kidney discharges are separated from the liquid to conserve the water, may be carried to a greater perfection in desert snakes than in those living in humid regions.<sup>20</sup> Thus it may be that desert snakes do not excrete water to the extent found by Benedict in his pythons and other dwellers in humid regions. Bogert and Cowles (1947, p. 33) concluded that reptiles are able to absorb moisture through the skin when in wet sand, or lose it in dry sand.

Water is not only imbibed as a liquid, or secured in the form of the liquid contents of the prey, but also digestion and oxidation produce molecular changes in the solids contained in the foods, resulting in the production of so-called metabolic water (Babcock, 1912, p. 87; Miller, 1932, p. 201; Baldwin, 1937, p. 41). This, according to Babcock, is important, not only because of the water produced that might not be otherwise obtainable, but because metabolic water performs different chemical functions than does imbibed water (p. 88). Some of the molecules in the food are of the form  $C_x(H_2O)_y$ ; and when the carbon has been burned by respiration to  $CO_2$ , which is exhaled as a gas, the rest of the molecule remains as water (Miller, 1932, p. 201).<sup>21</sup> Or, in some cases, there may be a reduction in the ratio of  $y$  to  $x$ —in the change from dextrose to starch, for example—so that one or more molecules of water may be released for each molecule of the original substance transformed, even though  $CO_2$  may not be the end product (Babcock, p. 120). Some of the chemical changes involved in metabolism lead to the oxidation of hydrogen contained in the food, through respiration of atmospheric oxygen, so the weight of the metabolic water produced may actually exceed the weight of the solids in the food. Baldwin (1937, p. 41) gives the following figures for the grams of metabolic water produced by the complete oxidation of 100 grams of food: Protein, 41.3 g.; carbohydrates, 55.5 g.; fat, 107.1 g. The metabolism of fat during hibernation produces sufficient metabolic water to prevent dehydration.

To return to the rattlesnakes, creatures predominantly preferring arid habitats, we may conclude that while they do drink water when available, they can live for long periods without it, and the species that inhabit deserts probably exist almost exclusively on the moisture content of their prey. However, water conservation is of great importance, and it is probable that this induces nocturnality in desert snakes even at times when diurnal temperatures are below the lethal level, for the humidity in their subterranean retreats is higher than on the surface. Schmidt-Nielsen and Schmidt-Nielsen (1949, p. 183; 1950, p. 75) have pointed out that this humidity is important in determining whether the generation of metabolic water involves a net gain or loss, for the loss through respiration may exceed the gain.

Rattlesnakes in captivity will almost never drink milk, even though water be denied them, thus exploding a myth that has long been current (see p. 1257).

<sup>20</sup> Some desert mammals have improved water-conserving excretory processes, compared with dwellers in more humid regions (Schmidt-Nielsen and Schmidt-Nielsen, 1949, p. 182).

<sup>21</sup> Vorhies (1945, p. 497) has shown that the banner-tailed kangaroo rat (*Dipodomys spectabilis*) lives largely on air-dried foods, partaking of succulents less than other small desert mammals, and hence is largely dependent on metabolic water. It rarely has access to actual water to drink. The important point is that it seldom resorts to succulents for its moisture supply even though they are readily available.

## FEEDING RATTLESNAKES IN CAPTIVITY

The food given to rattlesnakes in captivity is likely to yield more information on their methods of killing and swallowing prey, and on the frequency with which they eat, than on the kind of prey taken under natural conditions. It is impossible to offer all of the species of prey occurring in a snake's natural habitat, and therefore stomach-content studies of wild snakes yield better data than observations on captives, which do not show any great discrimination as to the prey they will accept when hungry. This may be of species markedly different from anything available in their native haunts. Rattlers do, however, discriminate between animals as different as rats and toads.

The reptile department of the San Diego Zoo began operations in 1922. We knew nothing then of the feeding of snakes in captivity; and such further handicaps as the lack of an adequate food supply, together with the unfavorable conditions under which the snakes were kept, made for short-lived exhibits, even after we adopted suggestions courteously given by older institutions. With the completion of a new reptile house, and, more particularly, after the advent of C. B. Perkins to take charge, there was a complete reversal of conditions. By the exercise of intelligence and patience he has achieved results in breeding and raising snakes in captivity, and in longevity records, of which our local institution is deservedly proud. It is upon Mr. Perkins' observations and results that the following notes are largely based.

Rattlesnakes are nervous creatures, and are thus among the most difficult of snakes to feed successfully. There are both species and individual differences in their readiness to accept food; there are even differences between the members of a single brood. In such institutions as zoos, which usually have available many more snakes than can be exhibited because of space limitations, there is a natural tendency to eliminate the finical feeders in favor of those that will eat readily; the attendants have little time to waste on such fastidious tenants, whose poor condition through lack of food soon becomes evident. Only the rarest, irreplaceable species are retained if they fail to eat. But a regular feeder becomes a valued possession, since a good exhibit is thereby assured over a long period.

Even the rattlesnakes that eventually become regular feeders do not always accept food immediately after they have become accustomed to their cages. Among 17 rattlesnakes of 12 different subspecies, the length of captivity up to the time food was first accepted varied from 3 to 360 days, the several periods being as follows: 3, 4, 5, 6(2), 7, 11, 14, 16, 27, 47, 63, 78, 103, 160, 220, and 360 days. With exercise of patience and with proper conditions, especially of temperature, probably 80 per cent or more of captive rattlesnakes will eventually become regular feeders.

## EFFECTS OF CONDITIONS OF CAPTIVITY

Rattlesnakes will feed more readily in fairly large cages—say with a floor area of four by four feet—than when more confined, although at the San Diego Zoo many of the specimens retained for study, rather than for exhibition, eat readily and thrive in cages only one and a half by two feet. But crowding is to be avoided, since,

if the snakes are really hungry and in the mood to feed, it is difficult to see that each gets its share if they can interfere with each other.

Temperature conditions are especially important. At too low a temperature a snake is usually too lethargic to feed, and even if it does, will have difficulty in digesting the prey. Dugès (1879, p. 15) observed that at 50° F. or below rattlers that had fed would throw up half-digested food they had eaten about 15 days before. Too high a temperature causes discomfort and nervousness. Probably a range of 77 to 85° F. is best, with an optimum for most species at about 80° F. This is the temperature at which the cages are maintained at San Diego.

Although a certain degree of stimulation, such as waving the prey before the snake, may be effective in causing it to seize the food, too much excitement, especially of an unaccustomed nature, may have an adverse result, frightening it into refusal. Although some rattlesnakes will feed readily enough in the exhibition cages, others are disturbed by the people crowding up to the window, for which reason a blind is generally placed over the glass when they are fed; this also avoids complaints from the tenderhearted, even though the snakes are not offered live prey.

#### DEAD FOOD

The feeding of dead prey to rattlesnakes does not offer any particular difficulty and has many advantages, from the standpoint both of the availability of food and of the safety of the snakes. Rattlesnakes are occasionally found eating carrion in the wild so that the use of dead prey is not entirely unnatural. It has been the experience of Mr. Perkins that rattlesnakes which will feed at all, will almost as readily accept dead food as live. In one or two instances individuals had to be started on live food, but later became accustomed to eating dead prey. According to Kauffeld (1953, p. 130) captive snakes, accustomed to dead prey, may thereafter refuse live prey.

When rattlesnakes are fed dead prey, it is much easier to see to it that, in their excitement, they do not strike the wall of the cage or each other. The danger that a snake may be bitten by the prey is avoided. With dead prey it is a relatively simple matter to be sure that each rattler gets its share, and this without interfering with its cage-mates. Even so, the attendant must be on the alert to see that one snake does not take hold of a mouse that another has started to swallow, for if this happens one of the contenders will continue blindly swallowing until it has engulfed the other, sometimes with fatal results to itself because the meal is too large to be digested. At the San Diego Zoo we have had many experiences with rattlers that have tried to swallow the same prey simultaneously, and in one instance the danger was not noticed in time to prevent a tragedy. In this case one massasauga (*S. c. catenatus*) ate another. Although forced to disgorge the meal almost immediately, the swallowed snake died on the following day, and the swallower two weeks later. Other instances of this sort of cannibalism have been mentioned under reptiles as food (p. 616).

Bud Hathcock, then of Oklahoma City, thus describes such an occurrence:

We had to separate two rattlers yesterday. Both took hold of the same bird, and when the heads came together, the larger naturally started swallowing the smaller.

Occasionally the dead prey is held with a forceps and waved before a rattlesnake to attract its attention and instill interest, but more often to aid in proper prey distribution among the several inmates of a cage. The feeding of dead prey to rattlesnakes is sometimes used as the basis of a stratagem to increase the food supply through the addition of substances the snake would not ordinarily eat. This is desirable, as small mammals are often difficult to obtain. Some zoo-keepers stuff meat scraps into the dead rodents before offering them to the snakes. Dugès (1879, p. 15) tied strips of meat to the tails of his rats. Kauffeld (1935a, p. 129) used the schemes of putting strips of beef heart in a mouse cage to acquire the mouse smell or of dipping the beef in rat hair.

The following are some references to feeding dead animals to rattlesnakes: Beauvois (1799, p. 367), Dugès (1879, p. 15), Mitchell and Pocock (1908, p. 792), Hurter (1911, p. 214), Ruthling (1916, p. 27), LeRay (1930, p. 203), Kauffeld (1943b, p. 609), Fautin (1946, p. 294), Loewen (1947, p. 53), and Kauffeld (1953a, p. 129). Several of these authors mention the taking of the food even after putrefaction had set in.

#### METHODS OF FEEDING

A rattlesnake that is accustomed to captivity and is anxious for food is quite a different creature from the inert and lethargic snakes usually seen lying about a cage. He will come eagerly to the cage door when it is opened, and with raised head and darting tongue manifest a lively expectation. He will quickly seize the prey held before him with a pair of forceps and retire to a corner to swallow it. At such a time rattlers seem to have at least some of the alert intelligence with which they are credited in the popular mind. They even learn to distinguish between attendants, or probably the routine that they follow, showing more interest when the one who usually feeds them opens the door. In order to reduce the excitement when a cage is opened for cleaning rather than for feeding, the snakes are allowed to smell the shovel used for the purpose. They soon learn to recognize this and retire quietly to their corners as soon as they have sensed its presence. Falck (1940, p. 135), who kept a mottled rock rattlesnake (*C. l. lepidus*) in captivity for 14 months, has commented on the lively attention manifested when food was introduced into the cage, even though it might not be eaten.

When there are several rattlesnakes together in a cage, even though they are fed dead rats or mice that are presented to them individually with a pair of forceps, great care is necessary to prevent their striking each other. Such strikes are caused by excitement and primarily result from a desire to seize the food, rather than any wish to inflict injury on each other. Although rattlesnakes are virtually immune to their own or another rattler's venom, a fatality quickly follows should a fang accidentally penetrate the brain, spinal cord, or a vital organ of a cage mate.

It is seldom necessary or efficacious to leave the prey in the cage for more than an hour or so; if it is not accepted at once it seldom will be later. However, with some individuals, leaving the food overnight has proved effective, for most rattlesnakes are nocturnal, particularly in summer. Sidewinders (*C. cerastes*), the most consistently nocturnal of all rattlers, seem to show a preference for night feeding in captivity.

Lowe (1943, p. 58; Allen and Neill, 1950d, p. 8) has suggested a method by which some reluctant rattlers can be induced to eat. A small box, with an entrance hole adjusted to the size of the snake, is placed in the cage, and a stunned or dead mouse is put in the box. Also odorous mouse-nesting material is placed at the entrance to the box. Thus the stage is set to excite a rattler accustomed to hunting prey in holes, and the rattler will usually crawl in and eat. Hediger (1950, p. 136) has suggested stimulating rattlers to eat by giving them solutions of grape sugar, which he says they will lick off the end of a blunt tube; also, he advocates injections of insulin. Artificial stimuli of this nature have been found unnecessary at San Diego.

Every beginner must be cautioned never to leave a live rat overnight in a cage with a rattlesnake, unless there be plenty of food available for the rat, for otherwise the rat will kill or injure the snake. Many an amateur has been surprised next morning to find his rattlesnake minus a part of its head or tail; for a hungry rat will get food at any risk, and a rattlesnake, unless hungry and alert itself, seems no match for so active and intelligent a creature. We have had experiences wherein rats ate the tails of otherwise uninjured rattlers, indicating that the rattler was without sufficient feeling or energy to protect itself. Experiences of the same character are mentioned by many authors (see p. 1047). This is a matter of commonplace knowledge among all experienced reptile-keepers. When rattlesnakes are kept in large outdoor pits, instead of cages, and there are holes or rock crevices in which both snakes and prey may hide, it is often satisfactory to leave the prey alive, but food for the rodents must be provided or the snakes will be eaten.

Forced feeding of captive rattlesnakes is not recommended; it is a dangerous and seldom-successful procedure that should be resorted to only in the case of some rare specimen that cannot be replaced. When forced feeding is employed, it is customary to push several mice down a snake's throat by mounting them on a thin skewer or splint. The first mouse is fixed to the end of the skewer so as to cover the point, thus preventing injury to the snake; the rest are threaded on the stick behind, like chickens on a spit. Once they are down, the rattler's neck is constricted with the fingers and the skewer withdrawn. Often the snake will regurgitate the food. An attempt to prevent this by the application of some form of tourniquet about the snake's neck is seldom successful; or it may be too efficient and kill the snake. Sometimes a rattler may be brought through an illness by the administration of an egg-milk batter with a syringe, a type of forced feeding possibly justified.

#### FREQUENCY OF FEEDING

At the San Diego Zoo young rattlers are fed once a week for their first year, grown snakes every two weeks. If a young snake, when changed to a biweekly diet, becomes thin, it is put back on a weekly schedule. Old snakes that have become very fat, as they sometimes do, are fed every four weeks. The standard meal comprises one mouse or rat of suitable size, so selected as not to stretch the snake's mouth unduly. Newly born mice are fed to the smallest snakes, and the largest rattlers are given the biggest rats available. For feeding purposes, a mouse-rat farm, comprising albino mice and rats, such as are raised extensively for laboratory use, is maintained.

Snakes born at the zoo are fed after their first shedding, which is usually from 5 to 10 days after birth. Adult rattlers, fresh from their wild habitats, are tempted

with food from 2 to 20 days after establishment in their permanent cages, the time depending on the degree of nervousness shown by the snakes. Failure to take food the first time is never accepted as final. The use of dead food is the rule, as already mentioned.

The following data on seven adult snakes will serve to indicate the average frequency with which food was accepted when the snakes had become regular feeders: A western diamond rattler (*C. atrox*) was received on November 14, 1936, and first ate five days later. From then until its death on September 8, 1947, it fed 145 times, or an average of once every 27.2 days.

A red diamond rattlesnake (*C. r. ruber*) was received as a juvenile in August, 1936. It did not feed until January 6, 1937. From then until July 3, 1946, the last meal before its death on September 27, 1946, it fed 195 times, or once every 12.7 days on the average. This was a female; it mated February 2, 1942, and gave birth to young August 11, 1942. During this period of pregnancy it fed 11 times, the last time 15 days before the young were born. It resumed feeding 13 days after their birth.

A prairie rattlesnake (*C. v. viridis*) received November 24, 1938, first accepted food on January 9. From then until July 6, 1954—it was still living—it fed 249 times, an average of once every 22.9 days.

A southern Pacific rattlesnake (*C. v. helleri*) was received March 9, 1937. It shed on May 16, and fed on June 22. After that it ate 288 times, up to July 6, 1954, at which time it was still alive. The average feeding interval was 22.0 days.

A southwestern speckled rattlesnake (*C. m. pyrrhus*) was received December 4, 1939, and fed a week later. Subsequently, to the time of its death on September 4, 1951, it fed 195 times, the average feeding interval being 25.8 days. Through an error in keeping records, this snake was overlooked and was not fed for an interval of 8 months. This was 3 years before its death, for it resumed feeding without any harm being apparent. If we allow for this gap, the feeding interval is reduced to 24.5 days.

A timber rattlesnake (*C. h. horridus*) in captivity for 15½ years was fed at average intervals of 21.7 days; another that lived 11 years averaged 20.4 days between feedings. Both of these individuals, because they became obese, were only fed monthly during their final 3 or 4 years. Undoubtedly they would have eaten oftener had the food been offered them.

Quantitatively, these frequencies work out as follows: On the average, an adult rattler about 1 meter (3 feet 3 inches) long, and weighing about 500 grams (1.1 pounds), is fed a rat weighing some 125 grams (¼ pound) every 20 days. Hence there are about 18 feedings per year, so that these captive snakes eat about 4½ times their own weight per annum, and remain active and healthy on such a diet. This may be compared with the figure given by Fitch (1949a, p. 550) of a food requirement of twice the body weight for northern Pacific rattlesnakes in the wild, with a seven-month active season.

#### SEASONAL EFFECTS

In the case of captive snakes, shedding does not seem to interfere seriously with the feeding schedule. Rattlesnakes have been observed to eat within two days of shedding, and also one day after. Some will eat when the eyes are semiopaque—the

so-called "blue-eyed" stage that ends about two days before the shedding. Thus, the widespread notion that snakes will not eat during the shedding period is not borne out by observations of captive snakes, although in the wild, for protection, they probably do not roam abroad while "blue-eyed." After a snake has been fully surfeited with food it prefers to lie quietly in one corner of the cage.

The snakes at the San Diego Zoo are kept warm throughout the winter and consequently remain active, without an interval of hibernation such as they would experience in a natural habitat. They accept food as readily in the winter as in the spring or summer. Mr. Perkins advises me that occasionally one of his rattlesnakes has refused to eat during the winter months. This was the case with the western diamond rattler mentioned above, which twice failed to eat through a winter. Loewen (1947, p. 53) had a similar experience with a massasauga (*S. catenatus*) that he kept for nearly 14 years. Dugès (1879, p. 15) reported that his captive rattlers would not eat in winter or when shedding. But, at San Diego, captive rattlers, kept at a substantially constant temperature through the year, usually show no annual rhythm in feeding or metabolism.

Experience at San Diego with adult rattlesnakes indicates that an offer of food every two weeks, with occasional refusals bringing the average feeding interval up to 20 to 24 days, is adequate to keep them in good condition. Well-fed captive snakes become quite fat. The fat is not periodically consumed in a long hibernation as is the case with snakes in the wild, and probably they exercise less, since they have no need to search for food. In the case of obese rattlesnakes, the feeding periods are lengthened to three or four weeks, for it is believed that more frequent meals would actually be detrimental. At the other extreme are the rapidly growing youngsters, which require a weekly feeding schedule.

#### INDIVIDUAL AND SPECIES DIFFERENCES

Some young in a brood will eat readily, whereas others refuse, for reasons that are not apparent. This has been found true at San Diego of a number of broods of several different species. Kauffeld (1943b, p. 611) reports that one of each of broods of the Arizona twin-spotted rattlesnake (*C. p. pricei*) and the banded rock rattlesnake (*C. l. klauberi*) would not eat, while the rest did.

At San Diego, we have found some species differences among adult snakes. Speckled rattlesnakes (*C. mitchelli*) and sidewinders (*C. cerastes*) feed less readily than other species. This does not seem to be a matter of nervousness. Some snakes that manifest nervousness for months, or even years, by rattling whenever their cage is opened, eat as readily as those that have become quite tame.

Once a rattlesnake has become accustomed to feed in captivity, so that it shows expectation and interest when a cage is opened, it will eat almost any kind of small mammal or bird. Mice and rats are used at the San Diego Zoo because they are the easiest to raise. Rattlesnakes in captivity will eat white rodents as readily as they do the gray or brown creatures upon which they prey in the wild. In fact, at the zoo, we have tried them on mice artificially colored blue, green, yellow, or red, without any evidence that the color was noticed. At times of a shortage of rodents, defective baby chickens from the commercial hatcheries have been substituted with success. Almost any snake accustomed to feed on rats will eat chickens, although in one case—this was before dead food became the practice—a cage of prairie

rattlesnakes showed fear of the baby chicks, and would not go near them until they had first been killed. Lizards comprise a good food supply for small rattlesnakes, but they are seldom available when needed. Kauffeld (1943b, p. 609) solved this problem by keeping a surplus frozen in a refrigerator.

#### REACTIONS OF PREY

Much has been written about the intense fear shown by any animal that may be put in a cage with one or more live rattlesnakes. Our San Diego observations have been quite the reverse. Before we learned the advantages of feeding with dead animals, or found that patience and a proper cage temperature were more important than the simulation of conditions met in the wild, we were accustomed to place live creatures in the cages, including rats, mice, rabbits, birds, young chickens, and lizards. None of these showed any fear of the snakes, unless alarmed by some sudden movement of a rattler or the buzz of a rattle, should some snake be frightened into sounding off. On the contrary, they ran or hopped unconcernedly around or on the snakes, much more worried by their new surroundings than by the strange co-occupants of the cages. Similar experiences are mentioned by W. (1846, p. 63), Audubon and Bachman (1854, vol. 1, p. 60), Dugès (1879, p. 16), and Coahoma (1902, p. 263). The latter saw a rattler about to strike a chicken. The chicken pecked the snake on the nose, whereupon it withdrew and left the chicken victorious. Col. M. L. Crimmins observed that birds repeatedly lit on the backs of captive snakes and paid no more attention to them than if they had been inanimate objects.

Stern (1871, p. 557) reported that a rattler in captivity would play with a mouse for several hours before destroying it. This is a fantastic idea; unless a rattler has an immediate interest in feeding, or is afraid of a mammal or bird, he will ignore it.

#### LONG FASTS

It is well known that rattlesnakes can live for long periods in captivity without food of any kind. They will last longer if they have water to drink; also they will survive longer in humid than under dry conditions, and at low temperatures rather than high, for under such circumstances life processes are slowed down and tissue and fat consumption are reduced.

As early as 1615, Hernández (fol. 192<sup>r</sup>) reported that rattlers could live a year without food or water, and this statement was repeated in subsequent natural histories (e.g., Nieremberg, 1635, p. 269; Jonstonus, 1653, p. 27). Audubon (1827, p. 29) mentions a specimen that lived three years in captivity, refusing all food offered it. This record is to be considered doubtful, as Audubon was both credulous and unreliable in the snake realm. Harlan (1835, p. 133) mentions two timber rattlesnakes that lived two years at the Philadelphia Museum without food, and Traill (in Schlegel, 1843, p. 100) knew of two that lived 18 months. Seeman (1853, vol. 1, p. 119) tells of a Coronado Island *caliginis* that survived eight months in a glass jar. Duméril (1854, p. 233; see also Pellegrin, 1902a, p. 164; 1902b, p. 244; and Flower, 1925, p. 977) mentions a rattler in the Muséum d'Histoire Naturelle in Paris that fasted for 22 months, after which it fed regularly for 10 years. Stradling (1881, p. 148) tells of a rattler that lived a year and 11 months after its last meal. A. M. Jackley advised me that he experimented with several medium-sized prairie

rattlesnakes. The first one died at 15 months; the rest lasted about 16 months—one somewhat longer.

At the San Diego Zoo, C. B. Perkins had rattlesnakes, which refused food but drank water, that attained the following longevity records:

Eastern diamond ( <i>C. adamanteus</i> ) . . . . .	16 months, 5 days
Western diamond ( <i>C. atrox</i> ) . . . . .	16 months, 8 days
Red diamond ( <i>C. r. ruber</i> ) . . . . .	16 months, 10 days
Great Basin ( <i>C. v. lutosus</i> ) . . . . .	19 months, 7 days
Southern Pacific ( <i>C. v. helleri</i> ) . . . . .	15 months, 8 days
Southwestern speckled ( <i>C. m. pyrrhus</i> ) . . . . .	16 months, 12 days
Eastern massasauga ( <i>S. c. catenatus</i> ) . . . . .	23 months, 4 days

These snakes were kept at the reptile house temperature of about 80° F. There is little doubt that under the more favorable conditions of a lower temperature some individuals would survive for two years; and most specimens, if starting in good condition, would have no difficulty in fasting for one year. Of course, after a snake has refused food for a long time there is little chance that he will become a natural feeder, yet Perkins had a western diamond that, after a year of refusal, suddenly seized a rat intended for a cage-mate. After this it ate regularly. Wright reports a massasauga (*S. c. catenatus*) that ate for the first time 10½ months after it was captured. Duméril's rattler became a feeder after a fast of 22 months. It has been thought by some that venom secretion ceases during a long fast, but Dugès (1879, p. 18) saw a rat struck and killed by a captive rattlesnake that had fasted for six months.

FEEDING EXPERIENCES

A number of articles containing valuable data on the food consumption of rattlers in captivity have appeared. Storer and Wilson (1932, p. 169) have presented data on three northern Pacific rattlesnakes (*C. v. oregonus*). Live rats comprised the food offered; they were sometimes struck but not eaten, particularly if the snakes were disturbed. The snakes ate more readily in the spring and summer than in autumn; they were not offered food in winter.

Thomas (1934, p. 32) found that northern Pacific rattlers fed readily in captivity. He gave them gophers, mice, and small ground squirrels. One ate a mouse and gopher one morning, a gopher two days later, and was still hungry. Vorhies (1936b, p. 104) found that two good meals might suffice a rattlesnake for a year; however, the period of observation was hardly long enough to prove whether health would have been retained over a long period without more frequent feeding. Bryan (1939, p. 51) recommended feeding once a week, but only when temperatures are adequate for digestion. In his experience, rattlesnakes seldom survived forced feeding. Fautin (1946, p. 294) fed Great Basin rattlers (*C. v. lutosus*) a kangaroo rat every two or three days. Kunzé gave a captive timber rattler 40 mice in 8 months; it was never given more than two at a meal.

Falck (1940, p. 135) has reported on the feeding of a mottled rock rattlesnake (*C. l. lepidus*) while in captivity for 14 months. This snake showed a decided interest when food was offered. It was fed salamanders, frogs, white-footed mice, house mice, and voles. The interval between feedings averaged 13 days, with a range of 1 to 47 days. Food was occasionally refused.

Kauffeld (1943, p. 607) has reported on the feeding of two broods of rattlers of two small species, the banded rock rattlesnake (*C. l. klauberi*) and the Arizona twin-spotted rattlesnake (*C. p. pricei*). One brood contained four, and the other six young. They were first offered pieces of mice, one of which was eaten. They refused mealworms, small grasshoppers, earthworms, salamanders, and small snakes. They fed most readily on small lizards, a prey known to be an important part of their diet in the wild. These were first offered alive, but it was later found they would readily eat them dead, either taken from a forceps or found lying in the cage. They sometimes showed a fear of live lizards. They were offered food at weekly intervals. One of each brood failed to eat. As the snakes grew, they were fed small mice or rats; *lepidus* showed a preference for mice with hair, *pricei* for hairless. They accepted food that had been frozen for preservation and then thawed.

Loewen (1947, p. 53) has reported on the feeding of a massasauga (*S. catenatus*) that lived in captivity 4 days less than 14 years. It was probably a year old when caught. Feeding records were kept during the final 11½ years of its captivity, during which time it fed 193 times. It seldom fed oftener than once a week; the maximum meals in any one month were six. During the nearly 12 years of the record it ate 135 mice, 89 sparrows, 3 chicks, 3 lizards, 2 field mice, one young rabbit, one mole, and 14 pieces of meat. The largest single meals comprised two full-grown sparrows, or three to four large mice. It fed readily on dead prey. During the summer it fed at an average interval of 11.4 days; it refused to eat in winter although kept at room temperature. The average date for the first feeding in the spring was April 9 (range Jan. 25 to May 25), and, for the last in the fall, Oct. 24 (range Oct. 5 to Nov. 17). This snake apparently died of senility.

Several of my correspondents have supplied interesting experiences in the feeding of captive rattlesnakes:

I have had success with the feeding of a *C. adamanteus*. I first force-fed him on egg, milk, and vitamins. He took seven doses from March 4 to June 10. Then I got some mice, which I offered him. Since then (to August 22) he has eaten five mice and a chipmunk. The vitamins given were heavy in B and evidently produce an appetite. R. E. Gordon, Atlanta, Ga.



I had some experiences in feeding two captive Mojave rattlers at Muroc. After about two weeks in captivity without eating—a proffered live *Uta* was removed after being untouched three days—another live *Uta* was dropped into the cage. Immediately one rattler approached the moving lizard and suddenly struck, hitting it in the middle of the back and hanging on, instead of recoiling. It held on for a full five minutes. In the meantime, the lizard had twisted his head about and grabbed the rattler by the neck. When the rattler finally extricated his fangs from the lizard's back, he found the lizard firmly holding onto his neck. For the next ten minutes the rattler tried to scrape the lizard off. All this activity had by this time aroused the other dormant rattler, and it approached the pair with interest. Suddenly it struck and grabbed the rattler, not the lizard, in the neck directly back of the lizard's death grip. It, too, hung on and did not recoil. For five minutes the trio were thus occupied. The first rattler seemed to be oblivious of his attacker's grip, but continued trying to get the lizard off and made no effort to get rid of the other rattler. When the second rattler retired after withdrawing his fangs, the first continued brushing the lizard off and finally succeeded in doing so. Then he quickly swallowed it and coiled up in a corner for digestion. The second rattler appeared nervous after that, so a second *Uta* was captured and dropped into the cage. The unfed rattler lost no time in striking this lizard in the conventional fashion, and then, without waiting for the lizard to succumb, swallowed it while it still was struggling weakly. I doubt if the second rattler intended to strike his cage-mate; he was probably aiming for the lizard and missed.

A captive rattler (probably *C. v. nuntius*) I had at the Petrified Forest National Monument at Holbrook, Arizona, also fed upon lizards. These he would strike and then neglect for 20 minutes or so. In the interim the lizard would crawl off into another corner of the cage and die. Then the rattler would carefully track down the exact trail the dying lizard had taken, using his tongue like a dog sniffing the ground. *Lloyd M. Smith, San Diego, Calif.*



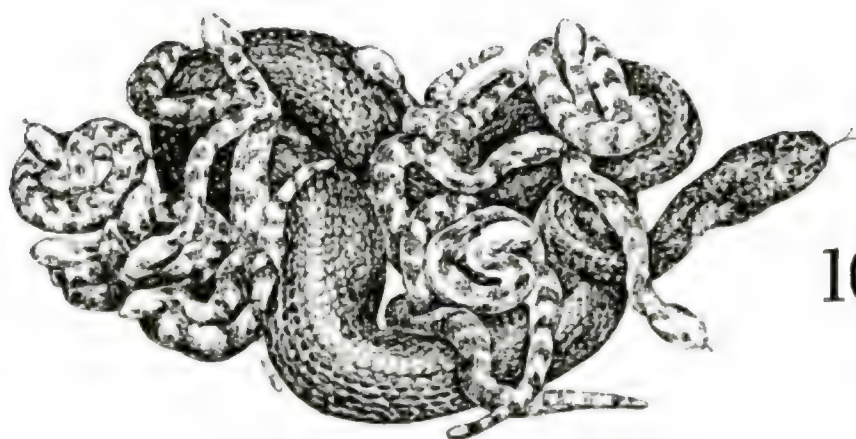
It was our custom to feed the rattlesnakes beef. This was done by cutting a wedge-shaped piece of beef and threading it on the end of a bamboo splint. The rattlesnake was held just back of the neck, the mouth was forced open, and the meat pushed down its throat. Then the fingers were tightened around the throat and the stick pulled out, leaving the meat inside the snake. No attempt was made to feed the rattlesnakes live food, as we had been told that they would not eat in captivity. This feeding was only done once in four or five days. *Bruce F. Stiles, Division of Fish and Game, Des Moines, Iowa.*



While at Zion National Park I had the opportunity of studying the Great Basin rattlesnake (*C. v. lutosus*). Its food included white-footed mice, wood rats, and chipmunks; and one captive rattler ate a side-blotch lizard (*Uta s. stansburiana*). I had several of these rattlers in captivity and found it an easy task to get them to take dead mice and wood rats, provided the animals had not been dead too long. One of the rattlers in particular would eat any mouse, if not too stiff, if it was dragged in front of the snake with a jerking movement. *Russell K. Grater, National Park Service, Estes Park, Colo.*



I had a large female sidewinder that ate two small horned lizards. I placed a large and vicious leopard lizard (*C. wislizeni*) in the cage one night. Next morning the lizard was inside the sidewinder. This was quite a mouthful for so small a snake. *A. C. Wallen, Los Angeles, Calif.*



## 10. Reproduction

### SEXUAL CHARACTERISTICS

Some kinds of snakes are oviparous—that is, they lay eggs. Others are ovoviviparous—that is, the eggs are retained in the body of the mother until they are ready to hatch, so that the young are born alive. The rattlesnakes are among those that give birth to living young.

In the southern sections of the United States, rattlesnakes normally mate in the spring, after coming out of hibernation, and the young are born between late August and early October. It is probable that the females give birth to their first broods at the time they reach the age of three years. In the more northerly areas, where there is a shorter season of activity and growth, the rattlers have a different life cycle, for it has recently been shown that they bear young only every two years, instead of annually. In these areas the young are born earlier than is the case farther south, that is they are born in the late summer, and mating may take place in the autumn. Studies of life cycles are complicated by the fact that female snakes may retain live sperm for a considerable time, and, in rare instances, a mating may not even be required for each brood.

### SEXUAL DIMORPHISM IN LENGTH

In general, adult female rattlesnakes are slightly smaller than the males. It is probable that snake genera in which the females grow to a larger size than males outnumber those in which the contrary is true, although examples of both may be readily cited. Thus the males reach a greater length in such genera as the patch-nosed snakes (*Salvadora*), the leaf-nosed snakes (*Phyllorhynchus*), the gopher or bull snakes (*Pituophis*), the long-nosed snakes (*Rhinocheilus*), and the moccasins (*Agkistrodon*). Examples of genera in which the females are longer are the California boas (*Lichanura*), the ring-necked snakes (*Diadophis*), the garter snakes (*Thamnophis*), the water snakes (*Natrix*), the lyre snakes (*Trimorphodon*), and the coral snakes (*Micrurus*).

Since snakes do not cease growing abruptly, as do mammals and birds, but continue a slow growth during the early years of their adult existence, it is difficult

TABLE 10.1  
SEXUAL DIMORPHISM IN LENGTH IN REPRESENTATIVE SERIES OF RATTLESNAKES

Kind of rattlesnake	Territory	Minimum size included, mm.	Number of adult specimens		Average length, mm.		Male superiority, per cent
			Males	Females	Males	Females	
Northern black-tailed rattlesnake ( <i>C. m. molossus</i> )	Arizona	700	150	28	955	862	10.8
Western diamond rattlesnake ( <i>C. atrox</i> )	Arizona	750	87	56	963	873	10.3
San Lucan diamond rattlesnake ( <i>C. r. lucasensis</i> )	Cape San Lucas, Baja California.	730	162	110	1,055	919	14.8
Mojave rattlesnake ( <i>C. s. scutulatus</i> )	Arizona	650	121	48	858	754	13.8
Prairie rattlesnake ( <i>C. v. viridis</i> )	Platteville, Colorado	650	224	170	776	737	5.3
Prairie rattlesnake ( <i>C. v. viridis</i> )	Pierre, South Dakota	705	179	178	862	822	4.9
Prairie rattlesnake ( <i>C. v. viridis</i> )	Warren Ranch, Wyoming	700	155	47	921	820	12.3
Great Basin rattlesnake ( <i>C. v. lutosus</i> )	Utah and Nevada	650	96	48	875	784	11.6
Northern Pacific rattlesnake ( <i>C. v. oreganus</i> )	Pateros, Washington	550	127	83	691	599	15.4
San Lucan speckled rattlesnake ( <i>C. m. mitchelli</i> )	Cape San Lucas, Baja California.	600	49	27	842	788	6.9
Colorado Desert sidewinder ( <i>C. c. laterorepens</i> )	Colorado Desert, California	440	91	58	540	562	- 4.1
Banded rock rattlesnake ( <i>C. l. klauberi</i> )	Southeastern Arizona	380	50	47	526	449	17.2

to fix standards of comparison between the sexes, for it is impossible to determine average adult sizes with the accuracy possible in the case of the warm-blooded vertebrates. If we determine the average sizes of the snakes that seem to be adults, we must arbitrarily fix the lower limit of what we choose to call the adult size, and the results are sure to be compromised by individuals that are extra-large adolescents on their way up to adulthood. We may, of course, compare the largest individuals available to us, or the average of the five or ten largest. Such results are fairly comparable, provided the sexes are equally represented in the series from which the selections are made, for it is obvious that the greater the number of individuals in a series, the nearer maximum size some of its members will be. It is always necessary in studies of this kind to be sure the material is territorially homogeneous, for there are differences in the ultimate lengths reached in different areas, even within a single subspecies of rattlesnake.

Elsewhere (Klauber, 1937, p. 21) I have presented the results of statistical studies of sizes of rattlesnakes, based both on large series of adult snakes and on the largest ten individuals available; and always, with the exceptions to be noted, the male rattlers were found to grow to a larger size than the females, in all subspecies of which adequate and representative series were available for study. The most recent data on the sex of the largest specimen that I have measured are given in table 4:1 of this work.

Some examples of the extent of sexual size differences, determined by studies of the largest individuals of each sex in a collection of snakes from a single locality, are as follows: Among 858 prairie rattlesnakes (*C. v. viridis*) from Platteville, Colorado (459 males, 399 females), the largest male was 1,015 mm. (40 in.) long, the largest female 863 mm. (34 in.); superiority of the male 17.6 per cent.

Of 117 prairie rattlesnakes from Warren Ranch, near Cheyenne, Wyoming (58 males, 59 females), the largest male was 1,258 mm. (49½ in.) in length, the largest female 1,000 mm. (39¾ in.); superiority of the male 25.8 per cent. The measurements of this series were received through the courtesy of George T. Baxter of the University of Wyoming.

Among 728 prairie rattlesnakes from near Pierre, South Dakota (375 males, 353 females), the largest male measured 1,076 mm. (42¾ in.), the largest female, 1,020 mm. (40¼ in.); male superiority 5.5 per cent.

Among 272 adult San Lucan diamondbacks (*C. r. lucasensis*) from Cape San Lucas, Baja California (162 males, 110 females), the longest male was 1,258 mm. (49½ in.), the longest female 1,127 mm. (44¾ in.); male superiority 11.6 per cent.

It must be admitted that although these statements as to the longest snakes found in certain groups are of some interest, the ratios representing the male superiority are statistically unreliable, since they are too dependent on only two individuals from each lot, either of which might be quite out of the ordinary, and unusual individuals are to be expected in almost any population.

Table 10:1, which shows the ratios between the average sizes of the adult males and females of certain territorially homogeneous groups of rattlers, is more consistent and dependable, notwithstanding the difficulty, already mentioned, of excluding all adolescents. When this table was prepared, an arbitrary minimum limit was set for each subspecies and all available specimens above that limit were considered adults.

In this table, we see that, except in the case of the sidewinder, the males consistently exceed the females in size by from 4.9 to 17.2 per cent. The mean difference is 11.2 per cent. The method of computation somewhat penalizes the males, since the setting of an arbitrary lower limit—if the males do exceed the females in length—will include more adolescent males than females in the assumed adult group. There is, however, a balancing factor, in that, in most of the series, there are more males than females.

The other method proposed, that of taking the mean of the ten largest of each sex, although eliminating one unfairness, introduces another, if the sexes be not equally represented in the available series from which the ten largest are selected; for the sex with the reduced representation will necessarily suffer in the comparison. Since the females are generally less adequately represented in collections than males, they are discriminated against. A study of this kind was presented in my earlier work (Klauber, 1937, p. 26). It was indicated that, with the sidewinder omitted, the other subspecies, where not less than ten adults of each sex were available, had an average difference in length in favor of the males of 17.6 per cent. The sidewinders are an exception, for in this desert species the adult females exceed the males in length by slightly less than 10 per cent (Klauber, 1937, pp. 24, 26; 1944, p. 98).

Sexual differences in size are not constant throughout the life cycle, for at birth the divergence is only about 1 per cent in favor of the males (Klauber, 1937, p. 12). The male superiority becomes about 3 per cent in juveniles at 8 to 10 months; and, in a composite population of adolescents and adults the males average about 5 per cent longer than the females. When fully adult, as has been shown, it is probable that adult male rattlesnakes exceed the females of the same subspecies by about 15 per cent. To this rule of male superiority, the sidewinders comprise the only exception, so far as may be judged from series available in numbers sufficient to produce reliable statistics.

#### SEXUAL DIFFERENCES IN PATTERN AND COLOR

It happens that the rattlesnakes most often encountered by the English settlers in the New World—the two subspecies of *C. horridus*—are subject to some sexual differences in pattern and color. As a result, this divergence, which is by no means invariable, even in *horridus*, was credited, for a time, to all rattlesnakes.

It was stated as early as 1709 by Lawson (p. 128) that the male rattler is distinguished by a black velvet spot on the head, and that it has a longer and slimmer head than the female. This observation, which is not accurate, was subsequently repeated by Lawson (1714, p. 133), Brickell (1737, p. 143), Brookes (1763, vol. 3, p. 368), and Goldsmith (1774, vol. 7, p. 209). Later, at least somewhat before 1800, the theory of a sexual color difference in *horridus* changed to the belief that the males were always black in color and the females yellowish (e.g., Atwater, 1838, p. 68). But as early as 1800, Tome (ed. 1928, p. 114) said that although the male *horridus* was often black and the female yellowish, this was not universally true; and the imperfect nature or even absence of sexual dichromatism<sup>1</sup> in this subspecies is now usually recognized (Netting, 1932, p. 12; King, 1939, p. 578; Clark, 1949, p. 260; Swanson, 1952, p. 181; Shorey, 1953, p. 25). Two observations on

<sup>1</sup> Noble (1937, p. 720) has stated that sexual color differences are rare among snakes.

the degree of the sexual color differences evident in *horridus* are the following. With regard to the timber rattler (*C. h. horridus*), as found in the Great Smoky Mountains, King (1939, p. 578) states:

A popular belief is that the yellow individuals are all females and the black ones all males. Upon examination this is not always borne out. The large yellow specimens usually are females, but infrequently males answer the same color description. The males tend to be darker in the posterior third of the body than do females, but females have been taken that were quite dark throughout. There are all degrees of variation between the yellow and dark phases, the yellow being more common locally.

Netting (1932, p. 12) thus characterizes the color differences of the timber rattler, as found in Pennsylvania:

Adult yellow or tan specimens are practically always females; black specimens are generally males, although black females are found occasionally. These color phases have given rise to the names Yellow Rattler and Black Rattler.

Rivers (1874, p. 505) thought the males of *horridus* in the Carolinas were lighter in color and slimmer than the females. He was certainly wrong on the color, for such color difference as there may be is in the opposite direction. The males are slimmer than gravid females, otherwise, except for the longer tail of the male, there is little difference in body shape. Adair and Ewbank (1922, p. 356) attributed diamond-shaped blotches to male eastern diamondbacks (*C. adamanteus*) and heart-shaped to the females, but no such difference is actually in evidence.

No sexual differences of importance have been found in the numbers of body blotches of rattlesnakes. Several large series were tested with the following results, expressed in terms of the coefficient of sexual divergence<sup>2</sup> in per cent: *C. atrox* 0.34, *C. c. laterorepens* -0.39, *C. r. ruber* 1.82, *C. r. lucasensis* 1.54, *C. s. scutulatus* 0.85, *C. v. helleri* -1.02, *C. v. viridis* (Platteville series) -1.62, *C. v. viridis* (Pierre series) -0.11. A negative figure indicates that the females average more blotches than the males. The differences are seen to be quite unimportant. For example, in *ruber* the males average 36.58 blotches and the females 35.92, or an average difference of only 0.66 blotch, and this is in the subspecies having the highest coefficient of those tested.

The sexual difference in the tail rings is almost always significant, for the males, with their longer tails, have more rings. Tests on large series involving 17 different subspecies of rattlesnakes indicated coefficients of sexual divergence of from 19.5 per cent in *lucasensis* to 36.6 per cent in *adamanteus*. The average coefficient for all forms was 26 per cent. But even with these wide and significant sexual differences, the tail rings are not of service in sexing specimens, since there is too much overlapping between high-count females and low-count males; and, more than in many characters, there is much subjectivity in counting the often indefinite tail rings.

Sexual differences in squamation have been discussed elsewhere in this work (p. 167; see also Klauber 1943a, p. 11, and 1945, p. 34). There are important divergences in ventral and subcaudal scutes, for the males have fewer ventrals and more subcaudals than the females, as summarized by subspecies in table 2:7. Such differences between the sexes as are found in other scale series are unimportant and not generically consistent.

<sup>2</sup> The difference between the means, divided by half the sum of the means, expressed in per cent.

## METHODS OF DETERMINING SEX—TAIL-LENGTH DIFFERENCES

Since no sexual color differences are evident in most rattlesnake species, and color dimorphism is not unfailing in the timber rattler, it becomes necessary to devise other means of distinguishing the sexes. As the anatomical differences cannot be ascertained with safety in live specimens, for handling would be required, one is usually forced to depend on a visual examination of the tail, which affords a dependable criterion in the case of adult specimens, especially after some experience has been acquired. The tail of the male is relatively longer and thicker than that of the female; also it tapers gradually from the body, whereas in the female there is a sudden and rather marked narrowing at the vent, which sets off the tail from the body (see fig. 10:5, p. 682).

When dealing with freshly killed specimens, accurate sexing is simple, for the hemipenes of the male may be extruded by a squeezing pressure, beginning at the base of the rattle and pressing forward. A caution is necessary with juveniles, in that the scent glands may be extruded and confused with hemipenes. The extruded scent glands are white and sharply pointed; the juvenile hemipenes are blunt and suffused with red.

In preserved specimens it is usually the practice to slit the tail of a specimen ventrally to determine the sex. The retracted hemipenes of the male will be found as a pair of thick, tendon-like processes extending from the anus toward the base of the rattle, and gradually tapering posteriorly. The scent glands of the female, which have led to some inaccurate determinations when the exploratory slits have not been long enough, will be found to terminate in rounded ends, only a short way back of the anus, whereas the hemipenes continue virtually to the rattle. It is of interest to record that in embryonic rattlers—and in other snakes and lizards as well—the hemipenes are extruded.

One method of determining the sex of live specimens is to probe gently through the anus into the tail with a blunt wire; the wire will readily enter more deeply into the tail of the male than the female (Schaefer, 1934, p. 181; Fitch and Glad- ing, 1947, p. 105). I have stated that the male tail is longer than that of a female having the same body length. This is a difference evident in nearly all species of snakes, but in the rattlesnakes it is not so obvious as in many other genera because of the relatively blunt tail that results from the attachment of the rattle. The extent of sexual dimorphism in tail length in rattlesnakes has been treated in chapter 4.

Several supposed sex differences have been mentioned by various authors. Lawson (1714, p. 133; Brookes, 1763, vol. 3, p. 368) says that male rattlesnakes have smaller and longer heads than females. I have investigated this theory (Klauber, 1938, pp. 3 and 36) and found that the females have, in fact, slightly larger heads at comparable ages, but the difference is so slight that it can be demonstrated only by careful measurements involving averages of many specimens. Certainly the difference could not be noted from a mere visual inspection.

Lanman (1863, p. 231) has stated that male rattlers have four fangs and females two. There is no truth in this supposition; individuals of either sex have two fangs on a side during the period wherein a functional fang is being replaced by a reserve fang. There appears to be no sexual dimorphism in fang length (Klauber, 1939b, p. 21).

### REPRODUCTIVE AGE

In 1937 (Klauber, p. 19) I made a study of the reproductive age of rattlesnakes and concluded that the first mating takes place in the spring when the females are two and one-half years old, and that they bear their first young when three years old. Also it was found that young females reach gravidity at about two-thirds of their final length. These findings were based on a study of several different species, particularly of their growth curves and rattles.

Subsequently Fitch in his studies of the northern Pacific rattlesnake on the San Joaquin Experimental Range in California, Jackley in South Dakota, and Rahn in his work on the prairie rattlesnakes of Wyoming, visualized a slower growth than my statistics of southern California forms would indicate. Rahn (1942b, p. 233) showed conclusively that the prairie rattlesnake (*C. v. viridis*) bears young biennially, at least in the northern parts of its range. Fitch (1949a, p. 539) and Glissmeyer (1951, p. 24) reached similar conclusions as to biennial cycles in the northern Pacific rattler (*C. v. oreganus*) and Great Basin rattler (*C. v. lutosus*), respectively. From these data it appears probable that in these northern areas the females do not give birth to their first young until the fourth anniversary of their own births, and sometimes not even until the fifth. But I am still of the opinion that among our rapidly growing southern species, the diamondbacks in particular, such as *atrox*, *ruber*, and *lucasensis*, the mothers bear at three years.

Among our rattlesnakes at the San Diego Zoo, a captive-born hybrid (*scutulatus* × *unicolor*) gave birth to young at the age of 43 days less than three years; and a Coronado Island rattler (*C. v. caliginis*), collected as a juvenile, had young at about its third birthday. And even in the northern forms, it is indicated by the sizes of mating or gravid females mentioned by Fitch and Glading (1947, p. 111) and Glissmeyer (1951, p. 25) that they may mate for the first time before reaching the age of three years. Then, on a biennial cycle, they would bear their first young at the age of four.

Volsøe (1944, p. 35) concluded that in Denmark the European vipers bear at the age of five years. Another worker, Bernström (Volsøe, p. 149) has concluded that they bear at four years. Conant (1933, p. 43) had a captive water moccasin that gave birth to a brood of young 2 years and 10 months after its own birth, which shows that other pit vipers may bear at 3 years.

### MALE ORGANS

The intromittent male organs of snakes are normally retracted into their tails and thus are hidden. They are paired, there being one organ on each side, and, in addition, each organ may be more or less bifurcated. Only one organ is used at a time. There are rather remarkable generic and even species differences manifested in the degree to which each hemipenis is bifurcated, and in the character of the exterior ornamentation in the form of fringes and spines. The ornamentation referred to is visible only when the organs are extruded for use, for it is only then that the fringes and spines are on the exterior of the organs. The organs are hollow, and in the course of being extruded via the cloaca, they are turned inside out. Thus the interior ornamented surface of the tube becomes the exterior surface upon extrusion. Extrusion and retraction are both accomplished by appropriate muscles.

*Use in Classification.*—As early as 1683, Tyson (p. 41, figs. 2, 3) accurately described and pictured the hemipenes of the rattlesnake. Schlegel (1837, vol. 1, p. 46; Traill's translation, 1843, p. 58) pointed out that the several kinds of snakes differed in hemipenial morphology. However, it remained for Cope, in a series of papers some 60 years ago (1893, p. 477; 1894, p. 833; 1895, p. 186; 1900, pp. 702, 1128, 1139, plates 12–31), to explore the nature of these variations in the hemipenes, and to propose their use, co-ordinated with differences in osteology and lung structure, as the basis for a new classification of all snakes.

Although the expectations of Cope as to the value of the hemipenes in classification have not been completely confirmed in subsequent investigations, they remain important nevertheless. It was once thought that, since they are presumably non-adaptive, any evolution in their morphology should be slow; they should be relatively stable and therefore likely to continue to show basic relationships. But Bogert (1940, p. 9) has pointed out that adaptations to specialized habitats have indirectly affected the hemipenes through modification of such characters as tail length, for example. Thus he believes that for the purpose of classification the male organs are more valuable at the generic level or below than at the subfamily level or above. Other recent discussions of the validity of these organs in classification are those of Vellard (1928, p. 406) and Clark (1944, p. 411). As far as the rattlesnakes are concerned, hemipenial characteristics are of decided interest and some importance in deducing specific and subspecific relationships. Because of the considerable specially prepared material available in my collection, I shall discuss some of the differences between species that are evident from these specimens.

*Preparation of Specimens.*—Hemipenes may be examined either *in situ* or extruded. The first position has the advantage of availability and simplicity, since every well-preserved adult male snake will furnish material for study. Furthermore, some important interspecies comparisons may be made by the correlation, for each species, of certain parts of the organ—such as its apex, point of bifurcation, and division of the sulcus—with the serial number of the superimposed subcaudal scale, counting backward from the vent. On the other hand, a properly extruded hemipenis can only be obtained just prior to preservation, while the dead animal is still pliable. But an extruded organ does have the advantage of permitting a study of shape; it also presents a clearer picture of the details and arrangements of the ornamentation than does a specimen *in situ*. If all possible differential criteria are desired, both methods of examination should be used.

As the production of properly extruded organs requires some experience, I shall outline the method that has been found satisfactory at San Diego, in the preservation of several hundred specimens. First, by pressure on the tail of a freshly killed snake, a partial eversion of one or both hemipenes is secured. Next the needle of a 50 cc. metal-barrel syringe, charged with ethyl alcohol, is introduced above the rattle with the needle directed forward, and pressure is steadily applied. This will usually cause a considerable eversion of one of the organs and sometimes both. The probability of full eversion will be improved if a string be tied tightly around the body just anterior to the vent. Occasionally it is found necessary to try several points of introduction of the needle until a fully effective vantage point is secured, especially with the larger specimens. As soon as it is certain that the apex

of an organ has been everted out of the neck, i.e., somewhat more than 50 per cent of complete eversion, a thread is tied around the neck with a single loop. By pulling on the thread, the neck is stretched outward to the utmost and is then cut off as close to the body as possible. The ends of the internal musculature (the retractors), that have been cut off are pushed up out of the neck and into the organ with a probe, so that they will not be held by the loop of thread.

The needle of the syringe is now introduced into the neck, and the thread is retightened on the needle. A gradual and firm pressure is applied to the plunger until full eversion is secured on both lobes. Full eversion in most species is usually evidenced by the appearance of a pointed apex. If each branch of the extruded organ takes the curved form of a ram's horn, the retractor muscle is being restrained by the thread loop and should be released. Care must be exercised that the needle, when introduced into the neck, does not puncture the wall; and the liquid pressure must be so limited as not to rupture the delicate apex. (This moderation of pressure will also avoid any distortion, since length-diameter ratios are of interest). With pressure still applied, and the thread ends under tension, the needle is withdrawn. The tying is then completed with a square knot, and the organ is ready for tagging and permanent storage in alcohol.

If both hemipenes are desired, it is necessary to secure eversion of both far enough to permit both to be tied off before either is cut away, otherwise, after the neck of the first is cut, leakage will render it impossible to secure sufficient pressure to evert the second. Although it is entirely possible to secure full eversion and distension without cutting the hemipenes away from the body, it is difficult to avoid their being crushed when the specimens are placed in jars for preservation. A complete amputation and separate storage are therefore to be recommended. The examination is also easier in the case of the separated organ. A method of preparation that involves the injection of hot paraffin into an extruded organ also produces an excellent specimen, although the process is somewhat more difficult than filling with alcohol. An early description of how the method is applied will be found in Ortenburger (1923, p. 71); see also Vellard (1928, p. 407).

*Hemipenial Characteristics in Rattlesnakes.*—The hemipenis of the rattlesnake may be described as follows: It is completely bifurcate, with a divided sulcus, one branch of which is carried to the apex of each lobe (fig. 10:1). The basal or proximal section is covered with stiff spines, particularly on the outer shoulders. Spines may or may not be present in the crotch. The spines are recurved, that is, directed backward. The distal, fringed surfaces of the branches may be laminate, reticulate, or partly of both forms. The borders of the frills are edged with spinules. The apices are calyculate. There may be a sharp, but soft, point at the apex.

Like other snakes, rattlesnakes manifest generic and species differences in hemipenes, whereby some of their relationships are clarified. The two genera *Crotalus* and *Sistrurus* are quite well differentiated, since in the former there is an abrupt boundary between spines and fringes, whereas in the latter the transition is more gradual.

The characters of the hemipenes that have been found useful in indicating specific and subspecific relationships are the following:

**Form:** The ratio of the length of each lobe to its diameter; the lobe shape, whether cylindrical or tapering from the spinous section toward the apex.

**Spines:** Their number, character, and spacing; the presence of small spines in the interspaces; the area covered by the spines, and particularly their presence or absence in the crotch; the abruptness of the change from spines to fringes at the boundary of the spinous area.

**Fringes:** Their number and whether laminate or reticulate; the presence of spinules on their edges.

Some of these characteristics are illustrated in figures 10:2a to 10:2h, which show several examples of hemipenes. Such variable characteristics as can be reduced to numerical or statistical form are the most useful for comparative purposes. But a study of hemipenes has disappointing features, for it is difficult, if not impossible,

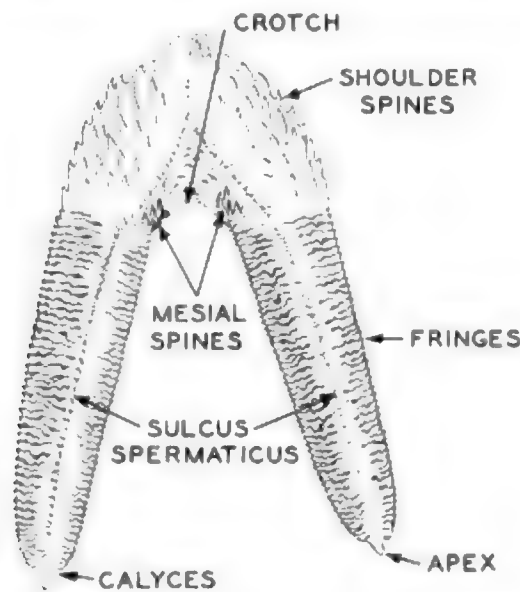


Fig. 10:1. Hemipenis of rattlesnake with the terms applied to characteristic features. Each male has a pair of these forked organs. When extruded, the sulcus aspects of the pair face each other across the vent.

to count some items objectively and uniformly; and, in others, intrasubspecific variation is so great as to mask intersubspecific differentiation.

For instance, the spines, although the most conspicuous feature of the ornamentation, are found unexpectedly difficult to count. Even when each spine tip is marked with a color to facilitate accuracy, by a touch with a violet copying pencil as the counting proceeds, the presence of numerous transitional points introduces great uncertainty. As to the size and shape of the spines, that is, whether long and thin, or short and heavy, differences are evident within a subspecies. There is also a considerable ontogenetic variation, not only in size and the degree of ossification, or hardening of the points, but in their number. Therefore the investigation must be limited to adults.

There is no approach toward an arrangement of the spines in rows, notwithstanding a fairly uniform scatter. Also the spines diminish in size so gradually, particularly on each side as the sulcus is approached, and along the proximal edge, that it is impossible to determine when counting should cease, for the end points, in considerable numbers, are mere spinules. In some species, particularly the *viridis* group, there is a further complication of smaller points scattered among the major spines. Attempts to count only full-sized spines are equally unsuccessful, so gradual is the transition. In *viridis*, about one-third of the spines are of prac-

tically full size; in *atrox* the proportion is larger. As far as possible, it was endeavored in these studies to count only those spines having raised, sharp, and hardened (ossified) points.

The spines are most prominent on the outer shoulders. They tend to decline in size near the sulcus, and likewise at the junction of the lobes in back. (The side with the sulcus is considered the front; actually it is the medial side, as the sulcus aspects of the separate hemipenes face each other across the vent.) In no species is there a junction of the two spinous areas across the back, but often there are many small spines near the dividing line. As a result of these uncertainties in spine counts, differences in counts are often evident between the two lobes of a single organ, as well as between the numbers counted on the two organs of the same snake.

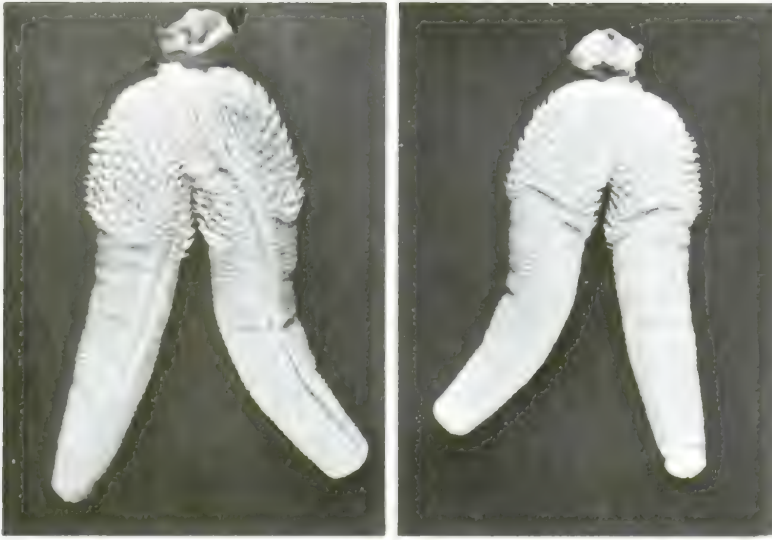
The fringes, on the other hand, may be counted with greater assurance. After a particular feature on the periphery has been adopted as a starting point—in this instance the most distal point reached by the spinous area (usually about 90° outward from the sulcus)—and a terminal point has been selected where the apical calyces begin, the count is fairly definite. A line toward the apex must be followed as the count proceeds, for the fringes tend to break and coalesce, and adherence to a single line is essential to secure an average. The counting is materially aided if the line be brushed lightly with a violet copying pencil, which makes the fringes more evident. This color subsequently disappears in alcohol. Care must be taken to count only fully everted specimens.

A distinction between laminate and reticulate fringes is useful, but involves difficulties, since there is a transition between the two; the straight laminations gradually become more wavy, until a netlike or honeycomb pattern is achieved. Often the fringes are laminated in front, that is, toward the sulcus, and reticulate in back. The apical calyces are moderately distinct from the fringes, even though the latter may, in themselves, be netlike.

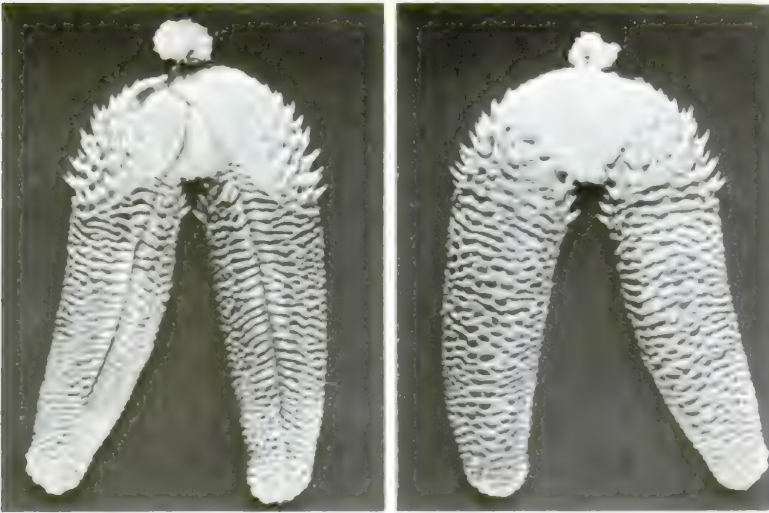
Where a sufficient number of specimens is available for several fringe counts, rather definite averages and ranges may be established for each species. In a series of 30 *atrox* the coefficient of variation of the number of fringes (average 57) was 4.3 per cent, thus showing good consistency. Ordinarily the fringe counts of most specimens will fall within three to five of the subspecific mean.

In an evaluation of the lobe shape, the length of a lobe is taken as the distance from the apex to the mesial point where the lobes branch; and the diameter is measured just distal to this junction. Specific differences are quite evident in these proportions, as exemplified by the short, thick lobes of *molossus* (figs. 10:2g and 10:2h) when compared with the long, slim branches of *adamanteus* (figs. 10:2a and 10:2b).

*Specific and Subspecific Differences and Relationships.*—Despite these uncertainties in counts and measurements, I think it worth while to present in table 10:2 some numerical data on the hemipenes, and to point out some of the species differences and likenesses that have been found. It is, of course, to be presumed that the larger rattlers would have more and larger spines than the smaller species, and also more fringes, and these suppositions are verified. The same trends are evident in stunted subspecies, as compared with their prototypes, as, for example, in a comparison of *nuntius* with *viridis*, or *muertensis* with *pyrrhus*.

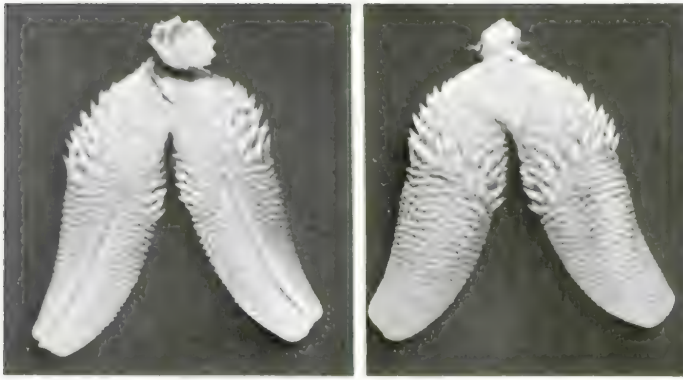


Figs. 10:2a and b. Hemipenis of *C. adamanteus* (both aspects), characterized by attenuated shape, plentiful thin shoulder spines, and extensive patch of mesial spines.

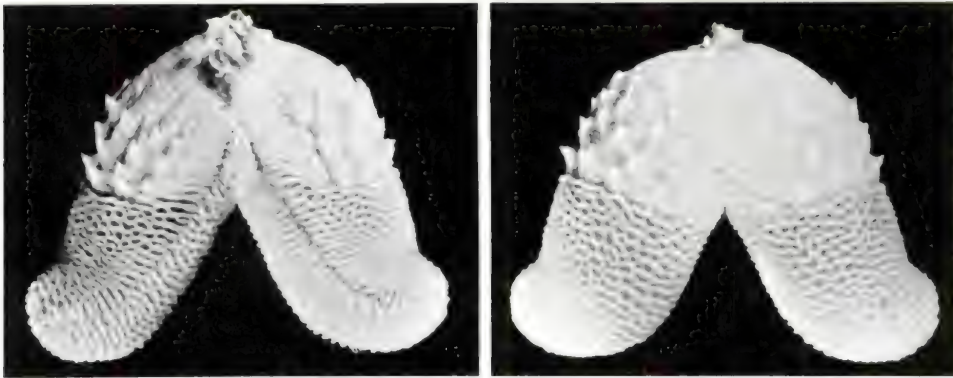


Figs. 10:2c and d. Hemipenis of *C. mitchelli stephensi* (both aspects), showing laminated fringes in front and reticulated fringes in back; few mesial spines; average attenuation for rattlesnakes.

In general, the results of the hemipenial investigation of relationships have been corroborative and confirmatory rather than novel. As already mentioned, the *Sistrurus-Crotalus* divergence is evidenced by a difference in the spine-fringe transition in the two genera—gradual in *Sistrurus*, abrupt in *Crotalus*. In searching for intermediates, we find only two, *C. stejnegeri* and *C. lepidus*. In *lepidus* this is probably only a chance convergence, rather than one with a firm phylogenetic basis,



Figs. 10:2e and f. Hemipenis of *C. enyo enyo* (both aspects), showing extensive patch of mesial spines.



Figs. 10:2g and h. Hemipenis of *C. molossus molossus* (both aspects), characterized by stout habitus and perfect reticulations in the rear; shoulder spines short and heavy; no mesial spines.

as is indicated by the fact that the intermediacy is more evident in *C. l. klauberi* than in *C. l. lepidus*, yet the latter, judged from pattern, is the more primitive of the two subspecies.

If we search out the species and subspecies that deviate from the rattlesnake mode, character by character, we find first, with regard to lobe shape, that the diamondbacks, especially *atrox*, have unusually attenuated organs, tipped at the apex with a soft pointed projection. At the other extreme, with short, thick lobes are *molossus* and *cerastes*, especially *laterorepens*. As to a marked taper, that is, a considerable reduction in diameter from the spinous to the fringed area, we find this especially evident in the subspecies of *C. durissus*, in *b. basiliscus*, and, to a lesser extent, in *horridus*.

In high numbers of spines, *adamanteus*, *basiliscus*, and *enyo* are outstanding, whereas some of the small forms have few, particularly *triseriatus* and *muertensis*. Although the shapes of the individual spines are difficult to assess because of fundamental differences in the size of the organ itself, we should designate *basilis-*

TABLE 10:2  
CHARACTERS OF RATTLESNAKE HEMIPENES

Subspecies	Ratio of length to diameter	Approximate number of spines per lobe	Average number of fringes per lobe	Spines in the crotch
<i>C. adamanteus</i> .....	3.5	202	51	many
<i>C. atrox</i> .....	4.2	64	57	few
<i>C. b. basiliscus</i> .....	3.5	162	36	many
<i>C. c. cerastes</i> .....	2.2	54	21	many
<i>C. c. laterorepens</i> .....	1.4	58	18	many
<i>C. d. durissus</i> .....	2.3	57	38	0
<i>C. d. culminatus</i> .....	.....	32	.....	0
<i>C. d. terrificus</i> .....	2.6	54	41	0
<i>C. d. totonacus</i> .....	.....	54	.....	0
<i>C. e. enyo</i> .....	2.3	134	33	many
<i>C. exsul</i> .....	.....	55	45	0
<i>C. h. horridus</i> .....	2.8	72	34	0
<i>C. i. omiltemanus</i> .....	1.7	22	14	0
<i>C. l. klauberi</i> .....	2.2	33	19	0
<i>C. m. mitchelli</i> .....	2.2	47	31	few
<i>C. m. muertensis</i> .....	.....	30	.....	0
<i>C. m. pyrrhus</i> .....	2.5	46	31	1 to 3
<i>C. m. stephensi</i> .....	2.8	60	31	1 to 3
<i>C. m. molossus</i> .....	1.7	68	21	0
<i>C. p. pricei</i> .....	2.2	51	22	many
<i>C. r. ruber</i> .....	3.1	55	42	1 to 3
<i>C. r. lucasensis</i> .....	3.1	62	50	few
<i>C. s. scutulatus</i> .....	2.6	49	40	0 to 2
<i>C. stejnegeri</i> .....	.....	.....	.....	many
<i>C. tigris</i> .....	3.0	64	40	1 or 2
<i>C. tortugensis</i> .....	4.3	95	50	few
<i>C. t. triseriatus</i> .....	1.9	20	20	0
<i>C. unicolor</i> .....	.....	80	35	0
<i>C. v. viridis</i> .....	2.5	92	37	0
<i>C. v. abyssus</i> .....	2.7	63	26	0
<i>C. v. caliginis</i> .....	2.5	40	31	0
<i>C. v. cerberus</i> .....	2.2	43	28	0
<i>C. v. decolor</i> .....	2.9	55	23	0
<i>C. v. helleri</i> .....	2.3	56	28	0
<i>C. v. lutosus</i> .....	2.5	57	29	0
<i>C. v. nuntius</i> .....	2.2	67	27	0
<i>C. v. oreganus</i> .....	2.1	57	27	0
<i>C. w. willardi</i> .....	2.6	56	16	1 or 2
<i>S. c. catenatus</i> .....	2.1	33	23	transitional
<i>S. m. barbouri</i> .....	2.4	.....	18	transitional

*cus* and the *durissus* subspecies as being outstanding for long and thick spines. *C. horridus* has long but thin spines. Short and thick spines are especially evident in *pyrrhus*.

Much more objective are the mesial spines—the patches or single spines in the crotch—and the closeness of their approach to the medial side of the sulcus. Such spinous patches are most extensive in *adamanteus*, *basiliscus*, *enyo*, *cerastes*, *pricei*,

and *stejnegeri*. From one to three mesial spines are usually present in *atrox*, *tortugensis*, *ruber*, *lucasensis*, and *exsul*; also in the *mittelli* subspecies—*mittelli*, *pyrrhus*, and *stephensi*. The *viridis* subspecies are characterized by a complete absence of mesial spines. In *Sistrurus catenatus* the mesial spines are transitional between true spines and fringes; in *S. miliarius* the spines border a mesial bare area.

It is quite evident that the number of fringes is dependent on the shape and size of the organ. The highest counts are found in the diamondbacks, whose hemipenes are both large in size and attenuated; those averaging 50 or above are *adamanteus*, *atrox*, *tortugensis*, and *lucasensis*. *C. m. molossus*, although a rather large rattler, has an average of only 21 fringes, clearly the result of its short lobes. Other species with relatively few fringes—*cerastes*, *klauberi*, *pricei*, *triseriatus*, and *willardi*—no doubt fall into this category because of their relatively small size.

If the rattlesnakes have a mode in the nature of the fringes, it is in a tendency toward laminations in front (the sulcus aspect) and reticulations in back. The species characterized by laminations throughout are *atrox* and its relatives (but not *adamanteus*), and also *enyo* and *klauberi*. Those with reticulations on both faces are *adamanteus*, the subspecies of *durissus*, and *cerastes*. The fringes are edged with spinules in all species; however these tiny points are fewer and blunter in *basiliscus* and the *durissus* subspecies than the rest. The gradual transition from spines to fringes in *Sistrurus* is effected by the presence of small, but definite, spines on the proximal fringes.

The rattlesnake (in the genus *Crotalus*) with the most singular hemipenes—the widest divergence from the rattlesnake mode—is the long-tailed rattler (*C. stejnegeri*). Its organs are not only longer and slimmer, proportionately, as might be expected from the long tail, but they are different in form, although deeply bifurcate as in all rattlers. The spines are small, slim, and very numerous. They cover the entire periphery of the lobe, except at the sulcus, and are present in the crotch. The transition to fringes is rather gradual, as in *Sistrurus*. The fringes are relatively small and disappear completely at the outer end, where the shaft is smooth and slightly expanded. A smooth area of this kind is found in no other rattlesnake, except that there is a longitudinal smooth strip located on the inner side of the crotch in *S. miliarius*, in which the strip is bordered with spines.

Some intraspecific differences are noted: Arizona specimens of *pyrrhus* have fewer mesial spines than other mainland forms of *mittelli*; and western subspecies of *viridis* have fewer spines and fringes than the eastern. Despite the extensive differences between the organs of *basiliscus* and *molossus* in shape, in the numbers of spines and fringes, and in the presence of mesial spines, when the problem arose of allocating doubtful specimens from southeastern Sonora and northern Sinaloa, the hemipenes were found of little value, since they were intermediate between the two forms as they occur at their centers of population. It will require further studies to determine whether this compromise has resulted from hybridization.

To summarize the more important indications of relationships and segregations derived from an examination of the hemipenes, I should include these: The corroborative difference between *Sistrurus* and *Crotalus*; the unique character of *stejnegeri*; the separation of *adamanteus* from the *atrox* group; the separation of *basiliscus* from *durissus*; the evident difference between *pricei* and *triseriatus*;

and both the within-group consistency and the evident, but not strong, between-group differences of *viridis*, *scutulatus*, and their fellows. I should pick *scutulatus* as the species with hemipenes nearest to the *Crotalus* mode.

The male organs, since they are both paired and deeply bifurcate, so that superficially there appear to be four when fully everted, have been the basis of statements to the effect that rattlesnakes have hidden legs (e.g., *Desert Magazine*, vol. 12, no. 6, p. 35, 1949). These legs are most likely to be evident, so it is said, when a snake has been singed in a fire.

## SEXUAL ACTIVITIES

### SEX RATIO IN POPULATIONS

In 1936, I made a study of the sex ratio in rattlesnake populations (Klauber, 1936b, pp. 8-13) and drew these conclusions, which have subsequently been strengthened by the researches of other workers:

1. At birth, the sexes are approximately equal in numbers.
2. There is a slightly higher mortality among the females, which leads to an excess of adult males of about 10 per cent.
3. Owing to a greater activity of the males, particularly in the summer and early autumn when the females are heavy with young, collectors capture more males than females, so that the adult males in collections average about 40 per cent in excess of the females.

Some statistics that verify these conclusions are as follows: Among 1,491 young-of-the-year (some of which comprised broods while the rest were collected at dens) there were 755 males and 736 females, a 2.6 per cent surplus of males. This is not a statistically significant departure from an equal division.

I have accumulated scale counts on more than 12,000 rattlesnakes of all species and ages; among these the males exceeded the females by 24 per cent. A tabulation of species shows this male surplus to be characteristic, not only of rattlesnakes generally, but of each individual species, or at least all of those of which medium to large series were available. If only adults are included, so as to eliminate the diluting effect of the juveniles on the statistics, the male surplus is usually between 40 and 50 per cent. Fitch (1949a, p. 520), in his studies of the northern Pacific rattlesnake (*C. v. oreganus*) at the San Joaquin Experimental Range in Madera County, California, found a male excess of 29 per cent among the young-of-the-year, and 40 per cent in the older population. Julian (1951, p. 21), in his work on the Great Basin rattlers (*C. v. lutosus*), determined the sex ratio to be unity at birth, but with 47 per cent excess males in the population as a whole.

Detailed studies of certain of the commoner species of rattlers have indicated a seasonal effect in collecting, for the male ratio in catches is particularly high in the summer and fall. Fitch and Twining (1946, p. 68) and Fitch and Glading (1947, p. 106) state that the activities of adult female northern Pacific rattlesnakes are much reduced from July to October. Evidently the females remain hidden while carrying young and thus escape capture. A. M. Jackley informed me that male prairie rattlers (*C. v. viridis*) were the first out of the dens in the spring; and

an early male activity has been observed among the southern Pacifics (*C. v. helleri*) and red diamonds (*C. r. ruber*) in San Diego County. However, it may not be true that the male surplus is only an apparent one because the gravid females remain concealed. Julian (1951, p. 21), in his studies of Great Basin rattlers (*C. v. lutosus*) at a den in Utah, learned, by marking and subsequently recapturing the same snakes, that the females are shorter-lived, on the average, than the males. Studies of European vipers by Volsøe (1944, p. 43) indicate the maintenance of a more even sex ratio throughout life than is evident among rattlesnakes.

Thus we may reiterate the conclusions reached in 1936: The sexes are born in equal numbers; females are subject to a slightly higher mortality so that the adult male excess is about 10 per cent; and, finally, females are concealed in the summer when carrying young and are less often captured by collectors, so that males exceed females in collections by about 40 per cent.

A study of the sex distribution within broods indicated that there is less of an evenly balanced distribution than would be expected from chance alone; that is, broods tend to run toward higher proportions of either males or females than would be expected from the binomial formula (Klauber, 1936b, p. 12).

#### TRAVELING IN PAIRS

Although the belief that rattlesnakes travel in pairs has had wide popular acceptance, probably abetted by the classic story in *Huckleberry Finn* (first ed., chap. 10, p. 80), it is not generally credited by herpetologists, except as possibly being true of a relatively short mating season.

The idea that various kinds of snakes travel in pairs is very old. Pliny (1855–57, vol. 2, p. 286; book viii, chap. 35; Topsell, 1608, p. 59; 1658, p. 434) stated that asps always roam in pairs, and that either would burst through any barrier to avenge an injury to the other. Bartholomaeus Anglicus (Steele, 1905, p. 142) said that the avenger could unerringly pick the culprit out of a crowd of men, a feature of the myth still current. These stories were often told of the European viper. However, the myth is world-wide; for example, Prater (1933, pp. 469, 473) mentions its application to the cobra in India.

As was to be expected, the finding of pairs of rattlers together, not an unusual occurrence in spring, soon led to the application of the tale to rattlesnakes. As early as 1752–53 Kalm (p. 317; 1758, p. 291) stated that rattlers were generally found in pairs; and this has since been reiterated unnumbered times (e.g., Bingley, 1803, p. 78; Tome, 1928, p. 115, but written about 1800) down to the present (McGuire, 1930, p. 93; Rutledge 1931, p. 646; 1946, p. 231).

A. M. Jackley had this to say about the frequency with which he had encountered paired rattlesnakes and the significances of such occurrences:

There is no evidence that prairie rattlers are inclined to leave the dens for their summer ranges in pairs, even though, to a considerable extent, they follow one another. When leaving the den, their immediate concern is to obtain food, and having secured it, they seek a safe place to stay until the food is digested. As suitable refuges are not plentiful on the prairie, such a resting place may become a gathering point for two or even as many as six. I find them in pairs more often in their mating season in September than in late May or in June. In fact, finding them in pairs between August 15th and through September is a common experience. [Mr. Jackley presented evidence to show that, in South Dakota, rattlers mate in the fall rather than in the spring, as is the case in southern California.]

Several of my correspondents affirm their belief that rattlers do usually travel in pairs:

It is my opinion that rattlers rarely travel alone. I have killed a great many and when you kill one you can usually find another within a radius of a few feet to a few hundred yards.



When I am working in a rattlesnake country during the mating season, and hear or see a rattlesnake, I always make sure there is but one snake before I try to kill that one, for I have had some narrow escapes from being bitten by the mate that was coiled and hidden close by, and did not warn me by rattling.



In the earlier days I killed many rattlesnakes and learned that often when I killed a large one, if I hunted around, I found another nearby.



Invariably when one rattler is found, another is close by. This is particularly true in August and September.

It should be observed that the story that rattlesnakes travel in pairs is both true and false; it is a matter of degree, for sometimes they do, but more often they don't. Rarely a rattler will be found lying beside another recently killed, and this has led to the belief that they do this invariably, awaiting a chance to avenge the late lamented.

That rattlesnakes may be, and frequently are, found together during the mating season is unquestioned; but that they travel in pairs at other times requires more than verification by an occasional encounter. Only the accumulation of a considerable body of statistics can verify a belief of this kind. Unfortunately, a person with a preconceived notion respecting a habit of this nature will unconsciously remember the occasions when two rattlers were found near each other and will forget the times when only one was observed. And again, when two are found together—which is not unusual—are they a pair? After all, rattlesnakes are somewhat gregarious, especially near the denning season.

Any territory, favorable from the standpoint of food and hiding places, is likely to contain several snakes, yet they may be entirely without attachment for each other; in fact we may be sure that creatures with so low an order of intelligence will have no such attraction outside of a brief mating season. It is doubtful that the many persons who have reported snakes seen traveling in pairs ever stopped to determine whether the two found together did indeed comprise a pair, or merely assumed this to be the case. On several occasions I have found two red diamond rattlers (*C. r. ruber*) together and they have almost as often been of the same sex as of opposite sexes. I remember having found two large king snakes together under a small piece of sheet tin in the spring. I naturally assumed that they were a mating pair, yet both proved to be females. Had such a check not been made, this would have been another verification of the habit of traveling in pairs.

Of course no one doubts that rattlesnakes are found paired during the mating season, and at this time a male will often be seen following a female. Fitch and Glading (1947, p. 110; Fitch, 1949a, p. 517), on the San Joaquin Experimental Range, reported that, in two successive years, the rattlers found in pairs comprised 26 per cent of all the adult rattlers encountered during the same period. Bogert states that paired trails are seldom seen in the desert by the professional collectors who follow trails as a fruitful method of catching rattlers. Mosauer, in his exten-

sive studies of the activities of desert reptiles, found only one instance in which a pair of rattlesnakes roamed about together (1935b, p. 21).

That rattlers always, or even frequently, travel in pairs is an exaggeration; that the survivor of a pair will untiringly and unerringly seek out and destroy the person who killed its mate is pure myth, for no rattler has the degree of intelligence implied. As for this myth, it has grown out of the fact that in the mating season a male occasionally has been seen to court a freshly killed female. From this small and unusual beginning have come the stories of the avenging rattler that follows the body of its mate over any devious course through which it may have been carried, until we come to the tale, said to be of Indian origin, of the human murderer who uses the vengeance of a rattlesnake to achieve his own by dragging the body of a dead rattler through the bedroom of an enemy, assured that the mate will follow. Several other stories of this type will be found in another chapter (p. 1244). Dalog (1897, p. 202) recounts the Venezuelan belief that if one rattler of a pair be killed, its mate will search out an herb wherewith to restore its life. The relationship of this myth to that concerning the rattlesnake, the black snake, and the dastardly onlooker (see p. 1241) will be recognized at once.

Clark (1928, p. 142) cites the traveling-pair story as an example of Mississippi-Florida folklore; and Brendle and Unger (1935, p. 200) list it as a belief of the Pennsylvania Germans. There is no doubt that it is believed in every section of our country. In the spring of 1954, a rattler was found in a downtown Los Angeles apartment. The snake was destroyed by an officer from the appropriate city department, but when a search of the premises failed to disclose the inevitable mate, the occupant left to spend the night elsewhere. Other references of some interest in this connection are Catlin (1868, p. 13), Kennedy (1942, p. 38), Devoe (1945, p. 486), Meek (1946, pp. 23-25, 133), Stimpson (1948, p. 287), and *Field and Stream*, (vol. 51, no. 1, p. 176, 1946).

#### THE MALE COMBAT "DANCE"

The combat "dance" of snakes—rattlesnakes among them—is an affair wherein the obvious isn't the truth, and the truth is stranger than the obvious. Even the title assigned to this weird performance is of doubtful applicability, since "combat" poorly describes a bout that nearly always ends in a draw, with neither participant injured; and "dance" is hardly appropriate to a sparring or wrestling match between creatures with neither arms nor legs. But the stylistic gyrations of the performers suggest a symbolic dance, and as the term "dance" has been applied to the exhibition by those who have most often observed it, dance it shall be, hereafter without the quotation marks.

The combat dance has been observed in several families of snakes and on all the continents, from which we may infer that it is an extremely ancient institution, going back to the dawn of snake history, before the ophidian world had differentiated into the dozen or more families and hundreds of genera that exist today. The reason this interesting performance has been so infrequently mentioned in popular accounts of snake activities is because the dance was thought to be an actual mating and therefore appropriate only to the more Kinsey-like types of scientific publications. This is why I used the word "obvious" in the introductory remark; snakes linked together or twisted about each other are obviously mating,

and so it was assumed, beginning with Aristotle (Creswell translation, 1862, p. 103; Peck translation, 1943, p. 423), down through the Arabian naturalist Damiri of the fourteenth century (Jayakar, 1906-8, vol. 1, p. 634), and Topsell (1608, pp. 9, 294; 1658, p. 802) almost to the present.

It is probable that one of the most ancient of insignia, the caduceus, which dates back to Sumerian times of about 2350 B.C. was originally based on fighting rather than mating snakes, as generally supposed (Budge, 1930, pp. 488, 490; Gershenfeld, 1930, p. 190). Brief histories of the caduceus and the evolution of its symbolism will be found in Howey (1928, p. 71) and Potter (1937, p. 7). The literature of this device, which has descended to us as a symbol of the medical profession, is very extensive.

The appreciation of the distinction between the male dance and mating came slowly. Vincent Richards (1885, p. 9; 1886, p. 12) recognized that male cobras would fight, while raised up anteriorly, and that "neither of the combatants ever seemed the worse for the fight." Kopstein (1914, p. 589) and Reuss (1926, p. 42) discussed male combats among vipers, and Reuss presented a series of photographs of *Vipera berus* males engaged in combat. McCann (1935, p. 400), in the case of the East Indian rat snake, and Fleay (1937, p. 40), in that of the venomous Australian black snake, demonstrated, by anatomical examinations of the participants, that intertwined pairs of these snakes, usually assumed to be mating, were actually both males.

As in other kinds of snakes, the dances of rattlesnakes were long assumed to be either matings or courtships preliminary to mating. Bromley (1934, p. 45) did describe an autumn combat between two northern Pacific rattlers; and Oren Arnold (1935, p. 133) observed that male rattlers wrestled with each other. However, it remained for Shaw (1948, p. 137; 1951, p. 149), Lowe (1948, p. 129), and Lowe and Norris (1950, p. 1) to appreciate fully and to distinguish the male dance from courtship and mating patterns, and to propose reasons for the dance. Other describers of the dance, some of whom thought it a part of the courtship pattern, while others (since the appearance of the Shaw, Lowe, and Norris papers) have understood that only males were involved, have been Davis (1936, p. 267), Lowe (1942, p. 261), Kennedy (1942, p. 191), Pequegnat (1945, p. 6), Gloyd (1947, p. 1; 1948, p. 1), Foree (1949, p. 5), Whisenhunt (1949, p. 1), Dayton (1949, p. 31), and Crites (1952, p. 60).

Some of the descriptions of the dance that I have received from my correspondents follow:

As often as 25 times or more, I have seen large specimens of the canebrake rattlesnake (*Crotalus horridus atricaudatus*) fighting, always in the fall of the year, and have watched these fights sometimes for as long as a half hour or more. Their method of fighting is to face each other, put the sides of the heads together, and gradually rear, still facing each other, with the necks in a half-turn around each other. When the snakes are as high as they can reach into the air, which in a large specimen will be as much as three feet, one will give a lurch upward and then bring its entire weight down across the neck of its opponent, slamming it on the ground with considerable force, evidently to injure the opponent. If the attempted damage fails, the snakes again rise in the same manner, and they will continue thumping each other against the ground until both become weary, whereupon they withdraw in different directions. In the many encounters which I have witnessed, I have never seen a snake injured or run away. The battle has always ended in a draw. *E. A. McIlhenny, Avery Island, La.*

In late July, 1928, while returning from an Arizona journey, I passed through the lower Laguna Mountains in San Diego County. It was late in the evening, sometime after sunset. One of the lads riding with me exclaimed, as we went past a roadside gully: "I just saw an octopus<sup>3</sup> lying there and it was moving its arms. However could it get here so far from the ocean?" "That's impossible," I said, but the lad insisted he had had no dream. Stopping the car, we walked back and there was, indeed, an octopus-like tangle of arms, but consisting of two rattlesnakes coiled about one another. They soon uncoiled and, now separated, began a most weird and gentle series of antics. The head and at least a third of the body of each was raised upright and, in a sort of rhythmic unison, they swayed back and forth before one another. Every few minutes, they would make passes at each other, embrace (neck and head separate) and then recede—only to repeat the odd performance. This we watched at close range with the serpents paying no attention whatever, either to our motions or spirited conversation. After about half an hour, it became so dark we could scarcely see them. *E. Jaeger, Riverside Junior College, Riverside, Calif.*



In July 1913, on Bower Mountain in Perry County, Pennsylvania, I was driving down the side of the mountain when I noticed, ahead of me, something unusual—two slim objects projecting above some grass along the side of the road. As I approached more closely, I saw they were rattlers. About half of the bodies of the two snakes were wrapped around each other like two ropes twisted together. The head and remainder of the bodies were in an upright position about four inches apart. The two snakes would lay their heads together for a few seconds then fly apart so quickly it was hard to catch the movements with the eye. This took place six times while I sat in the car with amazement, as this was the first time I had ever witnessed such a sight. Then, both snakes settled down into the grass by the roadside. I shot the two with a .22 rifle and when I walked a few steps to get a stick to place the snakes in the open road, a third rattler started rattling at me close by. He, too, met the fate of the others. *C. V. Dong, State Fish Warden, East Waterford, Pa.*



I once saw two snakes twined about each other, with heads way up in the air, going through a lot of foolish antics, bobbing around this way and that. I was mowing alfalfa hay at the time and couldn't make out at first what the object was that showed above the standing hay. But when I got closer, I saw it was two rattlesnakes. *J. Fred Toman, Bowers, Mont.*

Charles E. Arnold of San Diego has given me his notes on the dance of two northern Pacific rattlers (*C. v. oregonus*) seen by him four miles east of Coyote, Santa Clara County, California, at sundown on September 21, 1901. The snakes were raised well above the surrounding stubble which was about one foot high. The lower parts of their bodies were apparently twisted together, and the heads were lunging at each other.

The following observation is quoted from the report of the Death Valley Expedition (C. H. Merriam, in Stejneger, 1893, p. 215):

When passing through Emigrant Cañon in the Panamint Mountains in California, April 15, two large rattlesnakes were killed at one shot by Mr. Stephens, at an altitude of 1,400 meters (4,600 feet). They were on a ledge of rock, and were standing erect with their heads near together, apparently playing.

These rattlesnakes were of the subspecies now known as the Panamint rattlesnake (*C. m. stephensi*). I have examined the specimens, now preserved in the Smithsonian Institution, and found both to be males. Although Merriam did not state that these rattlers were mating, subsequent writers (e.g., Noble, 1937, p. 716), in reprinting the incident, have assumed that they were.

<sup>3</sup> Once, as I was driving along a hilly back-country road watching for snakes, I saw, lying on the pavement what appeared to be a dead octopus. Of course I backed up to make an examination. It was an octopus.



Fig. 10:3. Male combat dance of prairie rattlesnake (*C. v. viridis*). (Photographed 40 miles south of Mountainair, New Mexico, by E. W. Cottam. Published through the courtesy of the U. S. Forest Service and Mr. Cottam.)

Mrs. Harry Dayton wrote me, elaborating at my request, on a brief account of a dance that had been published in *Wyoming Wild Life* (vol. 13, no. 10, p. 31, November, 1949):

The observation of the queer rattlesnake performance was made last August on our ranch in the Little Bear country, 35 miles north of Cheyenne. We were quite a distance from the snakes when we became aware of a slight rustling sound, not like a snake's rattle, but just a whisper. Then we saw the snake heads up in the air about a foot apart. We watched them for several minutes while they lunged playfully at each other, twisted around each other, drew back and came close again, lay on the ground and raised up again, paying no attention whatever to us. We snapped two pictures. After a while the snakes started coming toward us, still apparently not seeing us, so we killed them.

The pictures of this incident show two prairie rattlesnakes (*C. v. viridis*), with their bodies rising vertically from the grass and with their heads facing each other (which required a 90° angle at the neck) at a distance of about six inches. I have seen several other photographs taken of dancing rattlesnakes in the wild, and it is easy to see how the wayfarer's attention is caught by these weaving vertical bodies, sticking up out of grass or stubble. Such a field photograph is presented here (fig. 10:3); this was taken by E. W. Cottam of two dancing prairie rattlesnakes found 40 miles south of Mountainair, New Mexico. Another photograph showed two western diamonds, as illustrated by Gloyd (1948, p. 1) and Force (1949, p. 5).

The most complete description, thus far published, of the dance as executed by captive snakes, was that of Charles E. Shaw (1948, p. 137). Mr. Shaw has been kind enough to prepare a condensation of his account, which is presented herewith, together with the photographs (figs. 10:4a to 10:4h) by G. E. Kirkpatrick that accompanied the original description:

On Friday, December 19, 1947, an adult male red diamond rattlesnake (*Crotalus r. ruber*) was added to the collection at the Reptile House and placed in a display cage with two other males of the same subspecies. The latter specimens had been born at the Reptile House on August 14, 1941, and were then approximately four feet in length. To our knowledge neither of these captive-bred males had heretofore attempted to engage the other in a dance.

On Sunday, December 21, 1947, about 4 P.M., it was noticed that the two captive-bred males were acting in a peculiar manner. It soon was obvious that we were witnessing either the initiation (fig. 10:4a) of a combat dance or a re-commencement of it after a short recess by the engaged males. The snakes faced in the same direction, one overlying the body of the other (fig. 10:4b). Both were nervously alert with tongues flicking out frequently, and heads and necks weaving rather slowly from side to side. The heads of both were held upward at an angle of about 45°. The uppermost male had the anterior portion of his body raised so that his head was held slightly behind and about three inches above that of the lower male, whose head and neck were raised only an inch or two off the floor. The upper male, lying with his body draped over that of his partner, lowered his head until it touched the other's head, whereupon the lower male immediately elevated the anterior third of his body to a height of 12 to 15 inches above the cage floor, the upper male rising simultaneously and maintaining his superior position. The raised portion of the lower male was considerably recurved so that only the top of his head contacted the ventral surface of the upper male (fig. 10:4c), both males apparently pushing (one forward, the other backward) against one another with a strong, even pressure. This position was maintained for a few seconds until the lower male lost his purchase and slipped off the ventral surface of his opponent. There was then an attempt of the snakes to entwine their necks, both making lateral undulatory motions with the raised portions of their bodies, while pressing against one another. Occasionally one participant was apparently caught off balance and pushed downward, but there was no evident attempt at this time by either male to throw the other forcefully to the floor.

p



c



p



a





f



h



e



g

(Photographs by G. E. Kirkpatrick.)  
Fig 10:4a to 10:4h. Episodes in the male combat dance of two captive red diamond rattlesnakes (*C. r. ruber*).

After several minutes of sparring in this fashion, the uppermost male left his position overlying the body of the other male, crawled over to a forward corner of the cage and then nosed along the glass front until nearly opposite the other male, which was lying flat on the floor and near the front center. At this approach, both snakes, about one foot apart and facing each other, assumed an elevated position again, the forward third of the body of each again being approximately 12 to 15 inches off the floor, the raised portions being strongly recurved and inclining at a steep angle, with heads held at about a 45° angle. There was little flicking of tongues after the dance was well under way. Both snakes weaved rather unsteadily from side to side in this awkward-appearing position, until the raised and recurved portions of the bodies were straightened vertically and then lowered toward one another until both snakes were touching scutes to scutes for a short distance several inches behind the head (fig. 10:4d). The heads were still being held at the 45° angle. At the moment of contact of the snakes, the entwining response was elicited, but neither male seemed inclined to force the raised anterior portion of the other to the floor in a violent manner; rather there was a continual lateral undulation of the raised bodies, neck twining, and untwining, a constant sparring, with an evident forceful pushing of the snakes against one another. With the forward part of the body still raised, one of the males turned away from his opponent and toward the window of the cage, pausing for a few moments in a raised position, motionless except for a peculiar rapid rippling muscular movement of the lower lateral surface of the neck about three or four inches behind the head. This combat dance was noted for approximately 15 minutes and its conclusion was not observed.

The recently introduced male was completely indifferent to the activities of the two combatant captive-bred males.

On January 4, 1948, again at about 4 P.M. (the time coincidence is indicative of our own activities, not necessarily those of the snakes) these two captive-bred male red diamonds were again noted while performing their combat dance. One of the snakes was definitely the aggressor, and the other snake, although joining willingly, did not initiate the dance. On this occasion there was more of the "scutes to scutes" position (fig. 10:4d) with the snakes facing each other, rather than an assumption of a superior position (fig. 10:4b), behind and overlying his opponent, on the part of the aggressive male. Both snakes had the anterior one-third of the body raised about 12 to 15 inches off the floor surface of the cage. The heads were inclined upward as before, the snakes remaining nearly motionless in this position for several moments, and then beginning what appeared to be an aimless swaying of the head and neck from side to side. Contact between the heads or raised portions of the bodies of the two generally brought about the neck-twining response with a slight sidewise or downward push of one snake by the other. Several times, with the anterior parts of their bodies erect, both snakes remained nearly motionless with their ventral surfaces in contact, to all appearances leaning upon each other for support. While in this position, the snakes were evidently firmly pressing against each other, until one or both lost purchase on the smooth contacting ventral scutes of the other and fell to the floor or nearly so (fig. 10:4e). These contacts did not result in the neck twining as is customarily the case when the snakes contact each other.

Sudden and forceful downward or sidewise thrusts of one male by the other were not noted until the aggressor apparently succeeded in twining his own neck twice about that of the other male. Immediately this advantage was achieved, there was usually a violent sidewise or downward throw of the opponent resulting from what appeared to be a quick lateral undulatory whipping movement by the aggressive snake. This motion is actually so sudden and rapid that it is difficult to observe the exact method by which one snake throws the other. The opponent was usually thrown violently downward to the floor of the cage, falling either upon his side or upon his back (figs. 10:4f and 10:4g). Occasionally this action was so powerful that the resultant whack of the snake's body on the floor could easily be heard, although the observer was separated from the snake by a distance of about 4 feet and also by the plate glass front of the cage. This dance was observed for about 25 minutes.

Subsequent to January 4, 1948, these two snakes were observed to perform the dance nearly every day. The pattern was essentially the same on all occasions. The same snake continued to be the aggressor in all dances. There also seemed to be more frequent violent

throwing of one snake by the other than had been noted previously. Sometimes the thrown snake fell to a position in which either his head or neck was directly beneath the body of the other snake. In these instances the snake responsible for the fall appeared to take advantage of the fallen male by firmly holding the latter's head or neck to the floor (fig. 10:4h). The fallen male invariably experienced considerable difficulty in extricating himself from this position. The victorious male, however, was never observed to follow up his success by inflicting any sort of punishment upon the fallen male, such as attempting to bite him.

Mr. Shaw (1948, p. 138) has this to say about the differentiation of the dance from the mating pattern:

An important and evidently overlooked difference between the courtship and combat-dance patterns lies in the degree of participation of the individuals concerned. Courtship involves extremely little or no overt response of the female to the male; she appears completely indifferent to the coaxing of her would-be mate. By contrast, however, the male combat dance involves vigorous performance on the part of both males, even though it shortly becomes obvious that one of them is definitely the aggressor (though not always the victor) during the entire dance.

Although the dance and mating patterns are so different that there is no difficulty in distinguishing them, for in the one case the rattlesnake's bodies are raised well above the ground, while in the other they lie beside each other, one published report—that of Whisenhunt (1949, p. 1)—mentions, in a single observation, attitudes characteristic of both activities. In this instance, although the snakes were mating, their swaying heads were raised off the ground about 18 inches. It is thought that they may have done this because they were disturbed by the intruder, or had temporarily lost their balance.

Published reports and letters from correspondents include the following species and subspecies of rattlers as having been seen to dance in the wild: western diamond (*C. atrox*), red diamond rattler (*C. r. ruber*), timber rattler (*C. h. horridus*), canebrake rattler (*C. h. atricaudatus*), Panamint rattler (*C. m. stephensi*), prairie rattler (*C. v. viridis*), southern Pacific (*C. v. helleri*), and northern Pacific (*C. v. oreganus*). There have also been indeterminate cases, that is, dances wherein the participants were unidentified, but that involved one or two of the three subspecies *C. v. helleri*, *C. r. ruber*, and *C. m. pyrrhus*. Many other observations of dancing rattlers have been made at the San Diego Zoo, the following subspecies having been seen to dance: *C. v. viridis*, *C. v. helleri*, *C. m. pyrrhus*, and *C. r. ruber*. W. T. Neill advises me that at E. Ross Allen's serpentarium in Florida, *atrox* is frequently seen to dance, but *adamanteus* does not dance.

The dancing pattern seems to be the same for all species and subspecies of rattlers. The snakes do not rattle during the dance. Bess Kennedy (1942, p. 191) watched a pair of western diamonds dancing and reported that they rattled, but she may have alarmed them. Richardson (1936, p. 45) and Jones (1947, p. 49) have reported that the victor eats the vanquished, which is certainly not true.

Dancing is not restricted to a single season of the year, as will be observed from these recorded dates:

March 13, *C. v. helleri* or *C. r. ruber*, at Miramar, San Diego County, Calif.

April 16, *C. m. stephensi*, Panamint Mountains, Calif.

April 20, *C. v. viridis*, near Harlowton, Mont.

July, *C. v. helleri*, *C. r. ruber*, or *C. m. pyrrhus*, Laguna Mountains, San Diego County, Calif.

July, *C. h. horridus*, Perry County, Pa.

August, *C. v. viridis*, near Cheyenne, Wyo.

September 21, *C. v. oreganus*, near Coyote, Santa Clara County, Calif.

December 6, *C. atrox*, Webb County, Tex.

One of the unfortunate results of the misinterpretation of the male dance has been to introduce uncertainties into the published records of mating dates.

There remains a difference of opinion as to the reasons for these stylized performances. They seem rarely to result in any injury. Bromley (1934, p. 45) found small head wounds on one of the participants of a dance, for their mouths were interlocked part of the time. Lowe and Norris (1950, p. 2) saw sidewinders actually bite each other in the neck during a dance, but no venom seemed to be injected, and no damage was done.

Shaw (1951, p. 166) is of the opinion that a homosexual behavior of one male toward another often initiates a dance. It may result from the lack of an adequate cue for sex recognition. The participants need not belong to the same species; in one case, over a period exceeding five months, a male southwestern speckled rattler (*C. m. pyrrhus*) repeatedly tried to mate with a male southern Pacific rattler (*C. v. helleri*), and whenever it did the southern Pacific would respond by taking the dance position, as if to convey a repellent cue. These rattlers had been caged together for several years before these dances took place.

Sometimes males have danced when there was or had been a female in the cage, but more often when no female had been present. Certainly the presence of a female is not necessary to stimulate males to dance. Once, in the case of three male prairie rattlers, dancing suddenly started after they had been cage mates for six years. There was no female present at any time. In another instance when two males had been together, the introduction of a third male caused the first two to dance. In one dance observed in the wild (Dayton, 1949) a third rattler of undetermined sex was present. In the occurrence described by Bromley (1934, p. 45) a female was said to be present near the sparring males, but whether the sex of the third snake was carefully determined is not known.

An observation made on some hybrid rattlesnakes (*unicolor*  $\times$  *scutulatus*) at the San Diego Zoo by Perkins and Shaw is of interest, since it may throw some light on the problem of the dance stimulus. There were four rattlers in the cage, three males and a female. One of the males was courting the female, which had just changed her skin. Whenever one of the noncourting males was held near the excited one, the latter immediately rose up to dance, to which the noncourting male would make no response. But whenever the excited male was given the shed skin of the female to smell, he would cease his attempts to dance.

Lowe and Norris (1950, p. 2), by a histological examination of two male sidewinders (*C. c. laterorepens*) that had engaged in a dance, found both to be in breeding condition. These authors believe that aggressive behavior on the part of snakes may be an expression of territorial defense, social domination, or sexual domination; also sex discrimination may be involved. But they do not draw a final conclusion as to the urge that leads to the rattlesnake dance. For myself, upon the evidence thus far adduced, I believe it probable that the dance stems from some sexual impulse, rather than from one based either on territorial defense or social domination.

## AGGRESSIVENESS OF MALES

Male rattlesnakes are occasionally aggressive during the mating season. Such a disposition was reported as early as 1723 by Dudley (p. 294). Mrs. F. D. Wood (1933, p. 86) came upon a courting pair of prairie rattlesnakes. She reported:

The noise of my climbing aroused the male and after a glimpse of me, he darted at me without pause, covering the eight or ten feet down the slope so rapidly and so unexpectedly that there was barely time for me to leap aside. His momentum carried him several feet farther down before he turned around. . . . In the author's experience with snakes of any kind, this male *Crotalus* was the only one to show real aggressiveness as opposed to the usual efforts to escape.

Other reports of the same character are as follows:

I have noticed rattlers mating during the latter part of the month of June and they were vicious and aggressive. *J. A. Rodriguez, U. S. Forest Service, Pecos, N. Mex.*



Rattlers are vicious during the mating season; otherwise they are docile unless hurt or antagonized. *Harry R. Wright, U. S. Forest Service, Waldron, Ark.*



A rattler on the point of capturing its prey is tense and alert; it will react at the slightest disturbance. The same is true of males at mating time, for then they are irritable, quick-tempered, and show anger without provocation. *A. M. Jackley, Pierre, S. Dak.*

Gillam (1916, p. 135) stated that he found two timber rattlesnakes (*C. h. horridus*) together, and the male seemed to cover the female's retreat.

## FINDING MATES

Noble (1937, p. 673), in thorough studies of the courtship and mating behavior of *Thamnophis* (garter snakes) and *Storeria* (brown snakes), showed sex recognition in these genera to be "accomplished chiefly by chemical sense, both olfactory and Jacobson's organs playing a part. Males distinguish the skins of their companions by their odor, both species and sex differences being recognized. The cloacal glands play no role in sex attraction or identification in *Thamnophis*. . . . Movement plays an important role during courtship." Baumann (1929, p. 36) has shown, that, in the Viperidae, it is the anal glands that probably play the major part in the finding of females by the males. These studies were continued by Kahmann (1932, p. 173; 1934, p. 249). Stebbins (1954, p. 15) cites the evidence of a collector that the glands are important in rattlesnake attraction. Bogert (1942, p. 262) has commented on the directness with which the sexes come together in the field. Chemoreception has been further discussed by Volsøe (1944, p. 23).

It is presumed, although adequate experiments have yet to be made, that in the rattlesnakes either the postanal glands or skin odors, or both, are important in the location of mates. The glands are larger in female rattlers than in males. That the sense of smell—that is, the tongue-Jacobson's-organs combination—is involved, is evident by the amount of tongue-flicking indulged in by an ardent male. Fitch and Glading (1947, p. 111) observed that, when a female *oreganus* that was being courted, suddenly escaped into high grass, the male searched for her by nosing slowly over the ground where she had been. Shaw, from his experience in finding it possible to stimulate a rattler to court with a freshly shed female skin, believes that the source of the stimulation lies in the skin rather than in the anal scent glands.

## COURTSHIP AND MATING PATTERN

In the course of the last 30 years, we have often had opportunities to observe the behavior of mating rattlesnakes at the San Diego Zoo. From notes on different species and subspecies, it is apparent that the pattern is quite uniform, both with respect to courting and copulation. Some typical instances will be described as examples.

I made the following observations on the courting procedure of a male red diamond rattlesnake (*C. r. ruber*) on February 12, 1937. The male was attempting to mate, but the female seemed unresponsive. He curled his tail under hers and

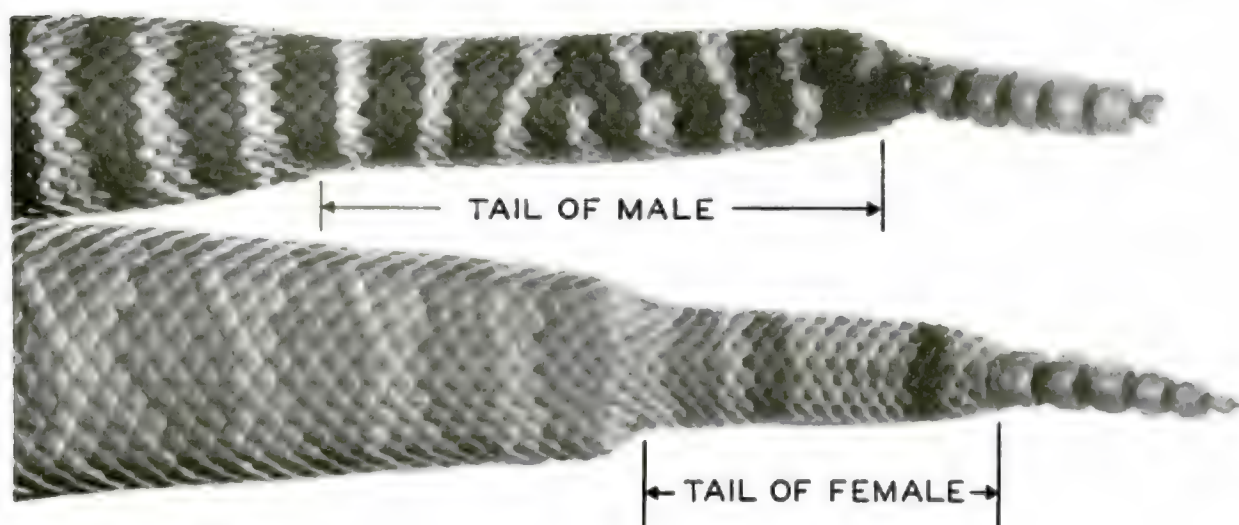


Fig. 10:5. Comparison between the longer tail of a male rattlesnake with the shorter, thinner tail of a female. The tail of the male is less sharply tapered from the body than that of the female. (The differences in pattern and color are not sex differences; the pictures are of snakes of different species but of almost equal body lengths.)

the posterior part of his body jerked convulsively forward. Neither snake sounded its rattle. The male's head was quite active, casting about in a somewhat indefinite way as if feeling or looking around, but usually along the body of the female. The female lay quiet. The male's tongue darted out frequently. The hemipenes were slightly everted. The tail of the male was curled first over the left side of the female's and under, then over the right. As the male was unsuccessful, he finally desisted. Several days later, C. B. Perkins observed a successful mating of the same pair.

A male southern Pacific rattler was observed to be courting on June 15, 1946. He was quite active, sliding along the body of the female and curling his tail under hers. The female had shed her skin the night before. The male's entire body made spasmodic jerks, not just the head as is sometimes the case. Where he had a coil in his body, a part of the circle jerked separately, which showed that the posterior part of the body was not just twitched forward by the head.

On August 1, 1946, a male  $F_1$  hybrid rattler (*helleri*  $\times$  *ruber*) was seen to court a female *ruber* that was quite unresponsive. He moved his head along her body with short (about one-half-inch) jerks. He had an intent and wide-awake attitude, quite different from the usual lethargic aspect of a caged rattler. The tongue was flicked

out frequently, but not in synchronism with the head jerks. His tail was wrapped around that of the female, and he also rubbed it on the underside of her tail several times. The head nudges were not made with the snout against the side of the female, but rather by his rubbing his chin along her back, pressing hard enough to move her skin slightly.

On May 12, 1948, I watched a courting southwestern speckled rattler (*C. m. pyrrhus*). His tongue was very active; frequently it was darted out, but did not stay out, nor was it vertically elevated or depressed, as in the pose of a rattler that threatens an intruder. Sometimes the tongue tips touched the body of the female, but not always. The frequency with which it was flicked out was at least once per second or oftener. While this was being done, the head of the male advanced with jerky movements along the female's back.

C. B. Perkins has often witnessed the mating of rattlesnakes in captivity. The following are his observations on several subspecies:

A female *ruber* that had been in captivity since sometime prior to June, 1936, was placed with a male of the same subspecies. A mating was observed 4 years later.

The male had been courting off and on since March 14, 1941, and copulation finally ensued between 2:15 and 3 P.M., March 26, 1941, and continued until 5 P.M. at least. Courting had been evident each spring since 1938, but no successful mating had been observed. At 4:40 P.M. there was a slight "breathing" or pulsating movement in the tail of the male. While locked, they moved around the cage to a considerable extent. They were separated next morning. The young were born August 14, 1941.

The same pair mated again the following year, on March 29. Efforts at mating had been observed as early as March 18. In this instance, the female seemed to require no urging, a condition not noticed in any other pair. Copulation was effected at about 11:35 A.M. At this time there was little movement. At 12:06 P.M. there was a slight pulsating movement in the tail of the male, no other effort being observable upon the part of either snake. At 12:30 the male changed his position; the same pulsating movement was evident. At 12:56 the male again changed his position with some pulsation. Both were otherwise quiet. At 1:30 the male moved again until his position was the same as at 12:30. Inspections were made at 2:12, 2:40, and 3:00, but no changes were evident. At 3:30 the female moved slightly and the male returned to his original position. At 4:45 they were seen to retain the same positions; there were no pulsations, although some had been evident up to this time. Observations at 5:22 and 6:07 showed no further changes. On the following morning, March 30, at 8:35 they were still locked together and no changes were observable at 9:30 or 9:40. At 10:15 they were seen to have changed position somewhat. At 10:45 the snakes were found to have parted; the right hemipenis of the male was still somewhat extruded, and this continued until 11:20. In this mating no nudging or courting movements upon the part of the male were seen at any time. The young resulting from this union were born August 30.

The same pair of red diamond rattlesnakes mated for the third time in captivity on March 31, 1943. They were first observed in copulation at 3:20 P.M.; it was not known when mating began. At this time they were motionless. At 5:50 P.M. they had not moved to any extent. At 9:50 on the following morning they were still locked. There was no movement observable except for an occasional pulsating or breathing motion in the tail of the male; there would be 3 or 4 pulsations and then quiet, with little regularity. At 11:40 they were watched for 15 minutes; there was a pulsating motion at the rate of about 20 per minute. The female changed the position of the anterior half of her body slightly from time to time. The male did some nudging. They remained unchanged at 12:30.

At 12:45 P.M. the female moved a little occasionally, dragging the male along for an inch or so. They parted sometime between 12:45 and 12:55. The right male hemipenis was still extruded and remained so (with some movement) until 1:45 when it was fully reverted. This was an unsuccessful mating. Seven eggs, evidently infertile, were extruded from time to time between August 18 and December 13, and one dead young, which appeared fully developed, was born November 29, 1943.

A pair of sidewinders (*C. c. laterorepens*) from the vicinity of Bensons Dry Lake, San Diego County, were caught on May 9, 1944. Next day the male was observed courting the female with the usual pattern—jerky head movements along her body—at 4:45 P.M. On May 11 at 9:30 A.M. they were found to be in copulation. At 10:00 A.M. the male was observed to be nudging the female at any part of her body that his head touched. He often held his tail straight up, waving it slowly in a circle. No pulsating or pumping motion was noticed.

At 11:00 they had moved halfway across the cage; from the activity it would seem that the male had dragged his partner. There was considerable motion in the entire body of the male, moving around and over the female. He still did considerable nudging with his head. There was no tail motion. For 15 minutes (11:15 to 11:30) they were watched continuously. There was little movement. At noon the male was almost motionless, except for tail waving. At 12:30 P.M. there was some nudging and tail waving. This continued at 2:15; both were crawling slowly with some dragging of the other. At 2:30 P.M. it was noted that the tail waving and nudging did not seem to be coincident.

At 3:00 P.M. there was a pronounced pulsating or pumping motion evident in the cloacal region of the female. The pattern seemed different (in the location of the nudging and in the tail waving) from other rattlesnakes observed. The cloacal region of the female was more swollen. At 3:30 P.M. it appeared that the pulsating motion was imparted by the female, although this was admittedly doubtful. It was at the rate of one per second for perhaps 10 seconds, then a little faster or slower until stopped entirely. The male yawned twice in a minute. At 3:45 P.M. it was observed the female was dragging the male almost continuously. He seemed to sidewind backwards. At 4:15 the female seemed to be trying to separate. At 4:50 they were still locked; the female coiled in a corner of the cage and the male stretched out away from her. On the following morning they were separated. As a result of this mating eight young were born on the night of October 13–14, 155 days later.



A pair of southern Pacific rattlesnakes (*C. v. helleri*) was observed in copulation at 9:45 A.M. May 7, 1944. The female had shed during the night. No courtship had previously been observed. The male had been in captivity since July 15, 1940; the female since January 2, 1941. When first seen to be locked, the snakes were quiet, except for an occasional pumping motion by the male, who also was nudging the female about six inches behind the head.

At 11 and 11:15 the female was dragging the male slowly about the cage. He seemed uninterested, but at 11:45 he was again observed to be nudging. At 12:15 the male was quiet, although the female was crawling. At 1 P.M. both were quiet. At 2 the female was again dragging the male. At 3 both were quiet although still locked. Sometime before 4 P.M. they had parted.

I have found two mating pairs of the sidewinder (*C. c. laterorepens*) in the field. The first was on April 21, 1935, in mesquite-topped sand hills one mile east of La Quinta, Riverside County, California. This was at 9 A.M. on a clear, warm day. They were found by tracking; they were lying quietly on the top of a dune in the shade of a bush. The tracks showed that there had been considerable joint activity nearby. The snakes were picked up in a net with as little disturbance as possible and were placed in a wooden box with a hinged cover. Thereafter, during the day (which was spent alternately in traveling and in hunting), they were examined hourly. They were beginning to separate at 4:25 P.M., and were fully separated sometime before 6 P.M. The left organ of the male was used.

The second pair was found at 8:50 P.M., May 6, 1939, on a branch road up Fargo Canyon, Little San Bernardino Mountains, Riverside County, California. There was a strong, cold wind blowing up the canyon; evidently they had sought the warmth of the pavement. Although carefully placed in a box they were separated at 9:20. Although without proof, I presume that copulation had begun the night before. Charles H. Lowe, Jr., found a mating pair of sidewinders at San Felipe, Lower California, on June 4, 1946, at 7:50 A.M.

L. M. Huey has given me the following data on a pair of red diamond rattlers found in copulation near Bonita, San Diego County, in early April: He was hunting birds' nests in heavy mixed brush and cactus, when he heard a loud rattling at a distance of about 20 feet. He found that this came from a pair of rattlers, which evidently had sensed his presence before he saw them. Although locked together at the tails, they both rattled vigorously. The day was bright, sunny, and warm; the time about 9:30. The snake's tails were at right angles, but both were lying stretched out on the ground, one with its head on one side of the bush, the other on the opposite side. Both were in the shade. When the snakes were killed they remained locked.

A. Pierce Artran reported a pair of red diamond rattlers found in copulation near Fallbrook, San Diego County. A second large male was nudging or stroking the anterior portion of the female. Similar trios have often been noted among various species of snakes in captivity. Fitch and Glading (1947, p. 111) and Fitch (1949a, p. 517), in describing the mating behavior of the northern Pacific rattlesnakes (*C. v. oreganus*) in the wild, state that they usually mate in secluded places, such as mammal-burrow entrances, rock crevices, or under the edges of rocks or bushes. One locked pair was seen to emerge from a squirrel hole. Mating pairs were sensitive to disturbance and quick to separate.

The following summarizes the mating pattern of rattlesnakes of the genus *Crotalus* as described by C. B. Perkins: The male courts by crawling beside or over the female; he nudges the female's body with an alert head, and his tongue is frequently darted out. Meanwhile the posterior part of his body jerks convulsively as the tail is curled under that of the female first on one side, then on the other.

The forked hemipenis on one side is everted slightly until finally the female's tail is raised and a successful admission is gained. There is no evidence that both hemipenes are ever used successively in a single copulation, despite the supposition of Milne and Milne (1954, p. 137) that they are.\*

After copulation has begun, a considerable pulsating or pumping action by the tail of the male is to be noted. This may be fairly regular or intermittent. For long periods both snakes may lie quietly with their bodies separated except at the tails; at others the male may continue a nudging courtship. Eventually the female seems to become restless and drags the male around until separation is finally effected.

Observations of matings in the massasauga (*Sistrurus c. catenatus*) by Guthrie (1927, p. 13) and our own at San Diego indicate that there may be divergences from the *Crotalus* pattern. When courting, the male jerks his head and flicks his tongue, as in the *Crotalus* pattern, but there is less nudging by the male; and in copulation there are longitudinal contractions of the male's tail, rather than pulsations as in *Crotalus*, and the tail of the female is more often held vertically.

Our studies indicate that copulation in the rattlers rarely lasts less than an hour or two, and probably 6 to 12 hours duration is more normal. One *ruber* pair remained locked for at least 22¾ hours, and another pair at least 19½ hours. One of 3 hours and 50 minutes was noted in *helleri*, and another lasted at least 5¼ hours. There was one of more than 7¼ hours in *pyrrhus*, two of more than 7½ hours in *laterorepens*, and one of more than 3½ hours in *catenatus*. Unfortunately it is sel-

\* Davis (1936, p. 276) reported successive uses of both hemipenes in a garter snake mating, from observations by A. C. Weed. Blanchard and Blanchard (1942, p. 223) doubt the accuracy of the observation.

dom that the times of both the start and end are known. Lowe (1942, p. 261) witnessed a sidewinder mating that lasted 2 hours.

It is evident that the mating pattern is frequently misunderstood. Although it has been stated that the anterior parts of the bodies may in rare cases be raised and intertwined, this position is certainly not normal in rattlesnakes. The male dance (see the previous section of this chapter) has often been inaccurately considered a nuptial performance. Also mere courtship has many times been reported as a successful mating.

The mating patterns of snakes show certain family and generic resemblances and differences, as described by Davis (1936, p. 257), Noble (1937, p. 673), Volsøe (1944, p. 22), and others. When the older references are reviewed, it is always necessary to distinguish mating behavior from male dances, for there is confusion between the two in many of the older reports.

The early travelers in America frequently supposed that the rattlesnakes found lying about dens were mating, since they were often found intertwined or even in such concentrations as to be referred to as "balls of snakes." Such ideas persist even to this day. For example, one of my correspondents writes: "I have seen rattlesnakes breed. They form a ball. I have seen a ball of snakes as large as a 30-gallon barrel. They also give off a terrible odor while breeding." Studies of large numbers of rattlesnakes at their dens by such observers as C. B. Perkins and A. M. Jackley have failed to verify any of these statements. At the San Diego Zoo we have had, in a single cage during the mating season, congregations of rattlers of from a dozen to several hundred. Although they frequently piled up in a corner of a cage until they reached a depth of a foot or more, no signs of sexual excitement were observed, much less a real mating.

A. M. Jackley reported that he had observed a male prairie rattlesnake that was endeavoring to mate with a decapitated female. Amaral (1932b, p. 93) has described the mating of a male jararaca (a South American pit viper, *Bothrops jararaca*) with a dead South American rattlesnake (*C. d. terrificus*). Schoettler (1950, p. 14) reported the mating in captivity of an urutú (another South American pit viper, *Bothrops alternata*) with a female *terrificus*. That male snakes court females of other genera and even of other families is not unusual among captives, but actual mating is rare. I have discussed hybrid rattlesnakes in chapter 4, including a single known intergeneric hybrid (*Crotalus* × *Sistrurus*). At the San Diego Zoo, a male gopher snake (*Pituophis catenifer annectens*) mated with a female southern Pacific rattler (*C. v. helleri*), which died shortly thereafter. I hope this evidence of abnormality will not be assumed to validate belief in the mythical bull-snake-rattlesnake hybrids current in the upper Missouri basin states (see p. 1267).

## FERTILITY

### REPRODUCTIVE CYCLES

It is somewhat difficult to generalize upon the reproductive cycles of rattlesnakes, since there may be not only variations between species, but also differences within species, produced by climatic differences. It is to be remembered that snakes are

immediately and strongly affected by air and ground temperatures, as well as by solar radiation; since they have no internal temperature-regulating mechanisms, such as those possessed by mammals and birds, their metabolic rates and muscular activities are at the mercy of external conditions, and hence are subject to frequent and considerable changes. This is particularly true when temperatures are approaching the lower limit of what is adequate for continued activity.

Although there are indications that in the southern United States rattlesnakes produce annual broods of young, this has not yet been proved. On the other hand, Rahn (1942b, p. 233) has shown that the prairie rattlesnake (*C. v. viridis*), in the northern part of its range, produces young every second year; for the season of activity and growth is so short that the offspring cannot be brought to full term within a single growing season. Since this same subspecies occurs as far south as central Texas, where the period of activity may be long enough for an annual brood to be produced, it is possible that there is a gradual change in the reproductive cycle from north to south within this single subspecies. Studies in intermediate territory should be made to determine whether some individuals follow an annual and others a biennial schedule, or whether year-to-year variations in climatic conditions affect the cycle in the population as a whole, so as to cause shifting from an annual to a biennial cycle or vice versa. A similar territorial variation in the reproductive cycle of the European viper has been discussed by Volsøe (1944, pp. 18, 149), who cites evidence of the prevalence of a biennial cycle in northern Europe and an annual cycle in the south.

It is also possible that in territories wherein both annual and biennial cycles occur, the smaller females may bring forth young at two-year intervals while the larger ones may be able to bring a brood to term within a year. This may explain the increase in fecundity with size that was found in the Platteville series of prairie rattlesnakes (Klauber, 1936b, p. 16).

A further complication that makes it difficult to determine the stages in reproductive cycles is the fact that female snakes can retain live sperm for a considerable time, and even a separate mating for each brood may not be essential. Sperm storage in various species of snakes has been discussed by Woodward (1933, p. 189), Kopstein (1938, p. 81), Trapido (1940, p. 107), Haines (1940, p. 116), Rahn (1940, p. 109; 1942b, p. 236), Blanchard and Blanchard (1941a, p. 163; 1941b, 187; 1942, p. 230), Ludwig and Rahn (1943, p. 15), Mrs. F. C. Blanchard (1943, p. 314), Volsøe (1944, p. 22), and Carson (1945, p. 223). The work of Ludwig and Rahn (1943, p. 15) is important, in that it describes the mechanism and effectiveness of sperm storage. Volsøe's paper contains significant data on seasonal fluctuations in spermatogenesis in the male European viper. Not only do these authors demonstrate that fertilization may not be coincident with insemination, which permits a wide latitude in copulation dates, but Kopstein (1938, p. 81) has shown that isolated female snakes have laid fertile eggs at intervals extending over as many as 22 months without reinsemination. Carson reported a female indigo snake that laid at least one fertile egg after four years and four months in solitary confinement.

A further complication in the fixing of mating dates lies in the undoubted confusion of mating with other activities. Thus statements, both in the literature and by some of my own correspondents, have confused mere aggregation of rattlers, particularly about the dens, with mating. Also the male combat dances, as

previously described, have been confused with mating. Combatant males are conspicuous because their bodies are raised above the ground.

Although it is true that there are seasonal differences between species, and that off-season matings may occasionally occur in any species, it is my opinion that along the southern border of the United States rattlesnakes probably mate each spring and the young are born in the following autumn. In the colder areas to the north, as demonstrated by Rahn, and no doubt at higher altitudes in the south, a biennial cycle prevails. In such a cycle, according to Rahn (1942b, p. 237), a summer or fall mating would fit rather well into the program of egg development. This would also substantiate A. M. Jackley's statement that the prairie rattlesnakes in South Dakota "mate only in late August and well into September."

In my own work on the prairie rattlesnakes, I found the two-year cycle confirmed in one series from South Dakota. This included 59 gravid females, of which 30 were in the stage that Rahn refers to as ripe, whereas the other 29 were in the *post-partum* stage. The yellow, developing eggs in the ripe females averaged 9.0 per snake; the small white eggs in the *post-partum* individuals averaged 18.4. Without doubt there was confusion in the latter case with the *corpora lutea*. Unfortunately, when I examined the Platteville series of prairie rattlesnakes from Colorado, Rahn's findings had not yet been announced, for which reason I failed properly to differentiate the eggs into two categories.

Fitch (1949a, p. 538) concluded, from an examination of the ova in northern Pacific rattlesnakes (*C. v. oreganus*) at the San Joaquin Experimental Range, that these snakes reproduce on a biennial cycle, for the eggs were found in the two different states of development during the breeding season. A biennial cycle, under the moderate climatic conditions in the foothills of Madera County, California, throws some doubt on the existence of an annual cycle farther south, at least among the subspecies of *C. viridis*. Glismeyer (1951, p. 25), from a study of the proportion of females with enlarged eggs in a series of Great Basin rattlesnake (*C. v. lutosus*) collected near Salt Lake City, Utah, concluded that these snakes reproduce on a biennial cycle, as would be expected from the climate of that region (see also Woodbury and Hansen, 1950, p. 68; and Burt, 1950, p. 12).

Rahn (1942b, p. 233) and Ludwig and Rahn (1943, p. 15) visualize the following course of a set of eggs in a two-year cycle: Small eggs are present in the ovaries in the summer and fall of the first year; they begin to grow rapidly during the summer of the second year and reach a large size (although still in the ovaries) when the snake enters hibernation in that fall. Ovulation, that is, transference of the eggs from the ovaries to the uteri, occurs when the snake emerges from hibernation in the spring, and at this time the eggs are fertilized by sperm that has been stored in special vaginal pouches since a mating during the previous summer or fall. The young are born in the late summer. I should judge that the studies of the Great Basin rattlesnake made by Woodbury's group indicate the same cycle of biennial egg development, except that they conclude that fertilization takes place directly from a mating in May or June (Glismeyer, 1951, p. 24; Burt, 1950, p. 12), and the young are born in August or September. Fitch (1949a, p. 539), in outlining the biennial cycle of the northern Pacific rattler, states that ovulation, and fertilization by stored spermatozoa, occur about two months after copulation in the spring.

Additional studies will be required to determine which species of rattlesnakes are on annual and which on biennial cycles. The requirement will be large numbers of fully adult females at the time they are entering hibernation in the fall. This will not be an easy collection to make, except where the snakes den together in large numbers, which, in itself, indicates a cold climate and a probable biennial cycle. But if the females of southerly species can be collected at that time, an examination of the eggs in the ovaries should settle the question. If almost all the females bear large yellow eggs, an annual cycle is indicated; if about half contain large yellow eggs, and the other half small white eggs, a biennial cycle is evident.

Observations at the San Diego Zoo indicate that rattlesnakes, under favorable temperature conditions, are quite capable of producing young on an annual cycle. For example, a pair of red diamondbacks (*C. r. ruber*) mated on March 26, 1941, and a brood of young was born on August 14. They mated again almost exactly a year later—March 29, 1942—and a second brood was born on August 30 of that year. There was a third mating on March 21, 1943, and a brood born on August 18, 1943; thus there was an annual cycle for three successive years.

In an annual reproductive cycle, if a sufficiently extensive season of activity and growth to consummate one be assumed, we should expect rapid egg growth in the autumn, following the birth of the previous year's young in early September. After a short hibernation the eggs would become fully enlarged by early or mid-spring, and ovulation would occur, followed by fertilization in a spring mating and the birth of the young in early autumn. I found (1936b, p. 21), from studies of *C. v. helleri* and *C. r. ruber*, that ova increase about 6 per cent in length and width during hibernation.

It will be noted that the additional time afforded in a biennial cycle is not consumed in an extension of the time between fertilization and delivery. It is required because of the long season of hibernation, which imposes a year and a half—in terms of calendar rather than active time—for egg growth prior to ovulation.

It should be observed that male snakes also have a reproductive cycle, the most complete studies of which were those of Volsøe (1944, p. 20) on the European viper (*Vipera berus*) in Denmark, and Petter-Rousseaux (1953, p. 209) on the European ringed snake (*Natrix natrix*). Volsøe found the males incapable of producing fertilization at the time of issuance from their dens from mid-March to mid-April, and that the end of April or the beginning of May must be considered the normal pairing time. He further concluded, because of the rapid reduction in mature spermatozoa, that late summer or autumn copulations would be ineffective. Volsøe believes that in more southerly climates spermatogenesis may occur earlier than in Denmark. The presence of pregnant females during hibernation does not prove that autumn matings occur, because of the prevalence of sperm storage among snakes.

Although no studies of spermatogenesis comparable to those of Volsøe have been made on rattlesnakes, it is known that the males do have seasonal cycles. Shaw observed a male *tortugensis* that suddenly indulged in a courting pattern, although it had long been separated from all other rattlers. To judge from the dates when most matings have been observed in southern California, spermatogenesis probably occurs earlier here than in colder climates. Cieslak (1945, p. 299) has shown, by experiments on garter snakes (*Thamnophis*), that the reproductive

cycle of both male and female snakes are correlated with the activity of the pituitary gland. Fox (1954, p. 415) has discussed the effects of climatic and other environmental factors on the timing of the reproductive cycles of male garter snakes.

#### BIRTH RATE

Birth rate statistics must be based on studies of the fertility of the adult females of a snake population. Confirmatory evidence may be obtained from size studies of large series collected at the dens, although, by the time the young snakes reach their first refuge, there will already have been a serious toll of the young snakes taken by enemies and weather. Furthermore there is evidence that, during their first winter, not all of the young repair to the dens used by the adults.

In 1936 (Klauber, 1936b, p. 14), I made studies and calculations of the birth rate of the prairie rattlesnake (*C. v. viridis*) in eastern Colorado, based on a large series collected at the dens, either at the time of their entering or leaving hibernation. Although unaware of the possibility of a biennial reproductive cycle, I did endeavor to distinguish between the developing yellow eggs and the small white ones. Rahn (1942, fig. 3, p. 237) has shown that in the hibernating season, when my statistics were ascertained, the yellow eggs are about 6 months from the production of young, whereas the small white eggs are 18 months away. Therefore, although, were I to repeat the investigation today, I should endeavor to make a more detailed classification of the egg sizes found, I think all the eggs I recorded as developing would have produced young in the subsequent summer or autumn, and therefore my previous figures remain valid. Of course, as I pointed out (1936b, p. 20), my figures are subject to whatever losses there would be between the number of eggs, as counted in the ovaries, and the final number of live young.

In this Platteville series, I found 1,767 developing eggs in 149 gravid females. This was in a total population of 841 snakes of both sexes and all sizes, including juveniles, which, at the next bearing season, would have become adolescents. This indicates a birth rate per unit of the total population of 2.10. If we make a deduction of three per brood for infertile eggs and defective young, the birth rate would be reduced to 1.57. This also presupposes no difference in the death rates of the several elements of the population between hibernation and the bearing season. In all probability the gravid females have a higher mortality than the rest of the population, which results in a still lower birth rate. Fitch (1949a, p. 599) reached the conclusion that the young northern Pacifics born each fall would equal 1.25 times the total rattler population that existed just prior to the advent of the young. Volsøe (1944, p. 29) found a birth rate among European vipers in Denmark of 1.02. His figures are derived from live young and therefore are on a sounder basis than mine.

#### SEASON OF MATING

I find the recorded dates of the mating of rattlesnakes to be rather confusing. There are species differences and also climatic differences, for where the snakes, because of their short active season, have been forced to the production of biennial broods, the entire reproductive pattern has been changed. There has been confusion of mating with basking at dens, with male combat dances, and with mere unconsummated courtship. There is also the complication introduced by sperm storage.

The red diamond rattlesnake (*C. r. ruber*), a distinctive and colorful species restricted to southern California and northern and central Baja California, undoubtedly mates in the spring. It has been observed in copulation in the wild on the following dates: March 7 and 8, April 2, 3, 13, 18, 20, and 26; and in captivity on February 12 and 18, and March 21, 26, and 29. A. E. Borrel (in Linsdale, 1932, p. 384) found a pair at San Telmo, Baja California, April 2, that may have been disturbed in mating.

The sidewinder (*C. cerastes*) is another southwestern species that usually mates in the spring. I found copulating pairs in the field on April 21 and May 6. J. R. Slevin found a mating pair on April 27. At the San Diego Zoo, a captive pair mated on May 11. But that autumn matings of this species probably occur in the wild, has been shown by Lowe (1942, p. 261), who found indications of mating on September 20 and October 18. A captive pair mated October 11.

A. J. Kirn found western diamond rattlesnakes (*C. atrox*) in copulation on April 13 in Texas. D. M. Gorsuch found a pair in Arizona that may have been mating on August 19, and A. A. Nichol saw a pair in copulation in captivity in May (Taylor, 1935, p. 154). Bogert (1942, p. 262) found a locked pair in the Coachella Valley on March 25. Mrs. Grace O. Wiley (1929, pp. 9, 11) observed matings of captive pairs on August 5 and December 29. The latter date was surely the result of the artificial conditions of captivity, as was another December date (4) recorded by Lederer (1936, p. 133).

Allen (1874, p. 69) saw two pairs of prairie rattlesnakes (*C. v. viridis*) mating in July. Mrs. Wood (1933, p. 85) found a mating pair in Wyoming on August 2. A courting pair was seen August 9. This seems to verify A. M. Jackley's conclusion that, in South Dakota, the rattlers mate in the fall. During one season, he reported having seen mating pairs as early as August 18 and as late as September 14. A captive pair in the San Diego Zoo mated on July 21.

But fall matings are not universal in the northern latitudes, as is evident from the following statement of P. J. Martin with regard to the habits of the northern Pacific rattlesnakes (*C. v. oreganus*) at the dens in the vicinity of Pateros, Washington:

I have observed them mating early in March and late in April, even to the forepart of May at the dens. I have also observed mating as late as May 15, after they had been placed in captivity. I have seen them in numbers in the lower country, after they spread out from the dens, but have never observed them mating there. Apparently mating is over by the time they start out on their summer's jaunt.

Fitch and Glading (1947, p. 110) and Fitch (1949a, p. 517) found spring to be the season of mating of *C. v. oreganus* on the San Joaquin Experimental Range. Mating pairs were first encountered about one week after the earliest rattlers had emerged from hibernation, and remained in evidence for some eight weeks (54 days in 1938; 36 days in 1939; 54 days in 1940). The mating dates, as was the case with emergence from hibernation, were found dependent on weather conditions. Not all of the Fitch-Glading observations were based on pairs actually seen in copulation; some pairs were merely courting or in close association. However the Fitch-Glading conclusions respecting the prevalence of mating during a relatively short spring season are unquestioned. But even in California, off-season matings, not to be explained as a misinterpreted male combat dance, are occasionally reported.

Thus Jasper and Wani Maris saw a pair of southern Pacific rattlers (*C. v. helleri*) mating on September 17, 1953. This was in the Palos Verdes Hills near San Pedro.

Some additional dates when captive rattlesnakes have been observed to mate at the San Diego Zoo have been these: Mexican west-coast rattler (*C. b. basiliscus*), August 31; Aruba Island rattler (*C. unicolor*), September 14 and 21; southern Pacific rattlesnake (*C. v. helleri*), May 7; Coronado Island rattlesnake (*C. v. caliginis*), March 5; eastern massasauga (*S. c. catenatus*), August 31, September 24, and November 8; *helleri* × *ruber* hybrid mating, February 2; *scutulatus* × *unicolor* F<sub>1</sub> hybrids, July 17 and November 9.

Mating reports subject to question are those of Winterbotham (1795, p. 406), who wrote that rattlesnakes mate in August, at which time they are most dangerous; Messeling (1953, p. 21), who says that timber rattlesnakes (*C. h. horridus*) mate in the fall; and Meek (1946, p. 263), to the effect that eastern diamondbacks (*C. adamanteus*) mate in mid-September.

It is my conclusion that along the southern border of the United States rattlesnakes normally mate in the spring, soon after they come out of their winter retreats. Where biennial broods are the rule, the mating times may be more widely dispersed, and summer or fall matings may even predominate.

In view of the variations that result from sperm storage and biennial broods, the gestation period is difficult to determine. I believe that in our southern California rattlesnakes the time averages five months (April 15 to September 15) or about 153 days. It is probably a few days less in the warmer areas and a few days more in the cooler or higher places. Fitch and Glading (1947, p. 110) estimated 172 days for northern Pacific rattlers at the San Joaquin Experimental Range. Some observations on the gestation periods observed at the San Diego Zoo have been as follows: *C. r. ruber* 141, 154 and 173 days; *C. v. caliginis* 174 days; *C. c. laterorepens* 155 days; *C. unicolor* 295 days; *scutulatus* × *unicolor* hybrids 170 days; *helleri* × *ruber* hybrids 190 days. As possible explanations of these highly variable intervals, neither the possible effects of sperm storage nor the high temperatures at the Zoo should be forgotten.

#### DATES OF BIRTH

Whether rattlesnakes bear young annually, as they evidently do in the southern section of our country, or biennially as in the more rigorous climates, it is probable that the normal birth time is the late summer or early fall, usually between August 1 and October 15, no doubt centering in mid-September. There is little question that the gestation period is influenced by temperature, even seasonal fluctuations having their effects. Thus, in the warmest areas of the desert, the young are produced annually and are born earlier, so that they have a better chance to secure food and so to survive their first hibernation. Where the season is long, but with summer temperatures usually below the optimum for snakes, as, for example, in coastal California, or at the higher elevations in the interior, the young are born later (about October 1 to 10), yet they still have a chance for survival because of the late advent of winter. Finally, in the areas of rigorous climates, where biennial broods are the rule, a relatively early birth can be effected, since the eggs are well developed by the spring preceding birth, and again the young have a good chance to feed before hibernation.

Whether off-season births occur among rattlesnakes, as do off-season matings, I do not know. I have occasionally seen rattlesnakes (especially southern Pacifics) in the spring that were so small it seemed they must have just been born. Had they been born at the usual time in the autumn, one could not imagine their having survived so long without either food or growth.

Births to mothers in captivity cannot be depended on to give natural-birth dates with entire accuracy because of the artificial temperature conditions, unless the mothers have been brought in shortly before parturition. Records of births in the wild are more conclusive, but unfortunately few are available. To find a brood with a mother is evidence that the young were probably born within a day or so, since they do not remain long with the parent. Continuous observation in any area will eventually show when the young-of-the-year are normally first in evidence. From years of records of young in the vicinity of San Diego, I believe that rattlesnake births are centered in the period September 10 to October 1, while on the desert side of the mountains they average a week or so earlier. In some states, August births are prevalent. The following are two incidents noted in my diary:

Henry Shelton told me of finding a brood of southern Pacific rattlesnakes (*C. v. helleri*) on September 20. He first found one or two crawling among some rocks he was overturning. Then under a large flat rock, he found the mother and a number of little ones, 11 altogether, including those that had been on the surface.



On September 18, E. V. Potter shot a large southern Pacific rattler at Japatul, San Diego County. It contained 10 young in capsules, evidently just ready for birth. One was liberated by the shot and this he saved, but the others were destroyed. This one lived until October 1, at which time it had not yet shed.

Fitch and Glading (1947, p. 110) and Fitch (1949a, p. 539) stated that the earliest appearance of young northern Pacifics (*C. v. oregonus*) varied with the dates of the issuance of the parents from hibernation in the previous spring. In one year, with a cold spring, the first young were observed on October 7, 171 days after the earliest record of mating; in another year with an early spring, the first young were found on September 11, 172 days after the first mating had been seen. One brood of this subspecies was born in captivity on September 20, in the San Diego Zoo. Glismeyer (1951, p. 24) believes that in the vicinity of Salt Lake City, Utah, the young of the Great Basin rattlesnake (*C. v. lutosus*) are born in August or September. A specimen at the San Diego Zoo had young on September 3.

As to prairie rattlesnakes (*C. v. viridis*), A. M. Jackley expressed the opinion that, in South Dakota, the dates when the young are born depend considerably on the annual differences in the weather. He thought that in years of heat and drought, most of the young were born between August 12 and September 5; in wet years the young were not in evidence until August 17, and some were not born until October 1. In a lot of eight gravid females from Montana, sent to Dr. H. K. Gloyd at the Chicago Academy of Sciences, the dates of birth of the young varied from August 31 to September 28; the median date was September 11. In a group of gravid females that I received from South Dakota, births occurred on August 14, 15, 18, 20 (three broods), 29, 30, and 31. One year A. M. Jackley sent me 79 young rattlers from Bonesteel, South Dakota, all of which were stated to have been born on August 21 to 23.

E. M. Cheuvront of Aliquippa, Pennsylvania, wrote me that female timber rattlesnakes (*C. h. horridus*) caught in early September gave birth to young on the following dates: September 15, 18, 21, 24, 25, 26; October 1, 8. Other birth dates for this subspecies have been reported as follows: September 6, 7, 12 (2), 18 (Ditmars, 1936, p. 370); September 13, 15 (Conant, 1938, p. 119; 1951, p. 119); September 8 (Trapido, 1939, p. 230); September 9 (Breckenridge, 1944, p. 159); August 26 (Edgren, 1948, p. 132). Clark (1949, p. 260) stated that the canebrake rattler (*C. h. atricaudatus*) in Louisiana has its young in late summer. C. F. Kauffeld advised me that a canebrake brood was born at the Staten Island Zoo, July 20.

J. T. Wright, of Tucson, Arizona, wrote me that three captive western diamond rattlers (*C. atrox*) gave birth to broods in late August. Gloyd (1937, p. 121) found a newly born brood of western diamonds in southern Arizona as early as July 30, and another on August 3. I once received from Hiram J. Yoder 139 baby western diamond rattlers whose mothers were collected in San Patricio County, Texas, shortly before they gave birth to their young. Mr. Yoder said that the young were born between August 15 and 20. Breedings of this species in captivity have led to births on June 4 (Wiley, 1929, p. 10) and July 19 (Lederer, 1936, p. 133).

Ross Allen of Silver Springs, Florida, advised me that captive eastern diamondbacks (*C. adamanteus*) gave birth to young on August 25, 26 (2), September 5, 11, 28, 29, and October 5. Other births known to me occurred on July 16 and September 14. Kauffeld (1943b, p. 607) reported banded rock rattlesnakes (*C. l. klauberi*) born on August 9, and Arizona twin-spotted rattlers (*C. p. pricei*) born on August 18. Stebbins (1954, p. 473) recorded that a specimen of *klauberi* gave birth to young on August 9, and a brood of *C. l. lepidus* was born on July 21. Dunkle and Smith (1937, p. 13) came upon several broods of Mexican black-tailed rattlesnakes (*C. m. nigrescens*) with their mothers on July 8, from which they judged that the little snakes had been born within a day or so. Stebbins (1954, p. 472) reported that captive sidewinders gave birth to young on October 15, and November 4 and 28.

Wright (1940, p. 221; 1941, p. 666) reported that captive eastern massasaugas (*S. c. catenatus*) from Illinois gave birth to young on August 17, 20, 30, 31, and September 1 (two broods). Swanson (1933, p. 37) mentions a brood born September 7. Breckenridge (1944, p. 152) and Conant (1938, p. 116; 1951, p. 116) each report a brood born August 6. Pope (1944, p. 221) has recorded a brood on August 30. It will be seen that all the massasauga births were concentrated within the 32-day period August 6 to September 7.

Some dates when broods of living young were born at the San Diego Zoo are as follows: Mexican west-coast rattlers (*C. b. basiliscus*) June 27; Mojave Desert sidewinder (*C. c. cerastes*) September 21 and 24, and October 15; Colorado Desert sidewinder (*C. c. laterorepens*) October 12 and 13, November 4; red diamond (*C. r. ruber*) August 10, 14, 18, and 30, and October 11 and 16; San Lucan diamond (*C. r. lucasensis*) January 15; prairie rattlesnake (*C. v. viridis*) July 27; Coronado Island rattler (*C. v. caliginis*) August 26; southern Pacific rattler (*C. v. helleri*) August 24, September 12, 17, 21, 24, and 27, and October 8 and 25; Aruba Island rattler (*C. unicolor*) April 5, May 13, June 5 and 27; eastern massasauga (*S. c. catenatus*) July 13, August 8, and September 3, 8, and 24; *helleri* × *ruber* hybrids, August 11; *scutulatus* × *unicolor* hybrids, June 10; and second-generation hybrids, January 10, March 20, April 4, June 18, and July 21.

Some other birth dates recorded from various sources are: Central American rattler (*C. d. durissus*) July 28; timber rattler (*C. h. horridus*) September 20; Omilteman dusky rattlesnake (*C. i. omiltemanus*) August 30; southwestern speckled rattler (*C. m. pyrrhus*) September 22; northern blacktail (*C. m. molossus*) August 7; Mojave rattler (*C. s. scutulatus*) August 22, September 18 and 20; central-plateau dusky rattler (*C. t. triseriatus*) December 1; southeastern pigmy rattler (*S. m. barbouri*) August 18; southwestern pigmy rattler (*S. m. streckeri*) August 10.

Summarizing these birth dates, we find that, out of 119 broods, 41 were born in September, and 41 in August, followed, in order of prevalence, by 12 in October, 9 in July, and 6 in June. The other 10, clearly off-season births, were scattered through 6 other months. There can be no doubt that most of the young of our Nearctic rattlesnakes are born in the last half of August or the first part of September.

#### PLACES OF BIRTH

Although some of my correspondents have expressed the belief that mother rattlers repair to the hibernating dens to have their broods, so that the young may readily locate the dens when the season for hibernation arrives, this is highly doubtful. Were all the mothers to have their young at the dens—this would be two to four weeks before denning time—it is obvious that the concentration of young rattlers thereabouts would be very high, which would reduce the possibility of their securing the food so necessary to their survival through their first winter.

A. M. Jackley had this to say about the habits of the prairie rattlers of South Dakota:

In the spring the females leave the dens with the rest of the population, and then late in August they find suitable holes or cavities wherein they give birth to their young. These places I call rookeries, since it is common to find a dozen or more females quite close together. The distances of the rookeries from the dens vary a good deal, but I think the majority are about half a mile from the dens, and rarely are they closer than 600 feet. I have noted only one instance wherein a female actually delivered her young at a den. Only a small proportion of the young spend their first winter at the regular dens. It is my conclusion that the young take refuge for their first hibernation in whatever holes they can find.

The habits of the females in those areas where no rocks are present and the snakes must necessarily den in prairie-dog towns, are somewhat different. But even here they do not use the regular dens as refuges in which to have their young, but seek out old dog holes on the outer edges of the dog town, holes that would have been closed except for the striped gophers or other rodents. They choose such holes in preference to the more open holes. Where the dog town is in somewhat rolling country, there are, as a rule, a number of old badger and skunk holes near the tops of the ridges. When that is the situation, most of the young are born in such holes.

In our more southern areas, where the snakes do not gather at dens from wide areas, but rather seek individual retreats for the winter, so likewise the females, when about to deliver, seek the most convenient rock crevices, mammal holes, brush piles, or other places that afford some shelter.

#### PARTURITION

Just as the discovery of snake embryos in mother snakes is the basis of many of the tales of snakes that swallow their young for protection, so the finding of eggs before the appearance of embryos has led to some of the mistaken statements that rattle-

snakes lay eggs (e.g., Lugger, 1883, p. 226; S., 1883, p. 7; I. Davis, 1889, p. 182; J. D. Mitchell, 1903, p. 35). Actually, the eggs are retained in the body of the mother until the young are ready to break out of the parchment-like flexible coverings. But the fact that rattlesnakes are ovoviviparous (live young produced in egg capsules), rather than oviparous (egg-laying), has been known since colonial days (Tyson, 1683, p. 26; Dudley, 1723, p. 294).

Hernández was told as early as 1615 (fol. 192<sup>v</sup>) that young rattlers were born instead of being hatched from eggs, but decided that those who had a contrary opinion were correct (see also Hernández, 1628, p. 329; 1651, p. 329; Nieremberg, 1635, p. 269). Guthrie (1927, p. 13) thought the idea that rattlesnakes lay eggs may have gained credence through someone's having seen a female extrude infertile eggs, as they sometimes do. But it is more probable that the belief stems from the fact that many kinds of snakes do lay eggs; or from the discovery of developing eggs in the body of a mother.

There are a few myths concerning oviparity in rattlesnakes. Meek (1946, pp. 23, 96) reports that diamondback rattlers lay eggs under rocks—that is the wild ones do; those in captivity bear living young. Tome (1928, p. 114, but writing in the year 1800) said that timber rattlers laid eggs (always in odd-numbered clutches) in the sand on river banks. After they had been in the sand for a month, the mother snake returned, swallowed them, and subsequently—or so it is to be presumed—gave birth to living young. And there is a story now going the rounds to the effect that rattlers east of the Rockies give birth to living young, whereas those to the west lay eggs.

There is a considerable variation in the intervals that separate the births of the successive members of a brood, although probably less in the wild than under the conditions of captivity, in which the spacing may vary from a minute or so up to hours or even days. When the brood comprises fully formed and live young, the intervals are likely to be shorter and more regular than where live young are interspersed with infertile eggs and defective young. In the latter case, the full delivery may take several months, whereas, under more natural conditions, the brood, often born at night, will be observed in its entirety on the following morning.

C. H. Pope (1944, p. 221), in observing the births of 8 eastern massasaugas (*S. c. catenatus*) in a brood of 11, noted that it required from 1½ to 8 minutes for the completion of each birth, and the intervals between births varied from a few seconds to 33 minutes. The newborn remained in the fetal membrane up to 9 minutes after delivery. Wright (1941, p. 666) reported a litter of 8 massasaugas, all born within an hour, or at an average rate of 7½ minutes per extrusion. Kauffeld (1943b, p. 607) noted that young banded rock rattlers (*C. l. klauberi*) broke their membranous sacs promptly and apparently without difficulty.

Trapido (1939, p. 230) has recorded the details of the birth of a brood of timber rattlers (*C. h. horridus*) to a mother that had been in captivity somewhat less than three weeks. This was on September 8, 1933. His observations may be summarized as follows:

1. Ten young were produced by a four-foot *Crotalus h. horridus* over a period of approximately 4½ hours during the middle of the day.

2. The intervals at which the young were extruded from the mother varied from 11 to 51 minutes, with an average of 33 minutes.
3. The period from the first appearance of the young at the cloaca to the time of complete extrusion varied from 5 to 25 minutes.
4. The time from the extrusion of the young to the rupturing of the fetal membrane may be as long as 43 minutes, or the membrane may be ruptured at or just before the actual parturition. Only the one that required 43 minutes seemed to experience any real trouble in getting out.
5. The coiled young ruptured the fetal membranes by a series of upward thrusts of the snout.
6. The umbilical stalk dried up and broke off within a day after birth.

In rattlesnakes, the point of attachment of the umbilical stalk is shown by a short longitudinal scar that crosses one or more ventral plates. It remains in evidence for some months.

Lederer (1936, p. 133) observed contractions in the posterior of a female before the birth of young, and that, as the young were born, rhythmic contractions of the body forced the remaining embryos toward the cloaca.

How protracted a more unnatural birth series may be, is shown by the following record of a red diamond rattler at the San Diego Zoo in 1941: August 18, two infertile eggs; September 8, one infertile egg; September 30, one infertile egg; October 4, one infertile egg; November 29, one dead young. Another record from the same species follows: At 9:10 A.M. August 14, 1941, it was noted that there were two premature and one live young in the cage, born during the night. Then followed at 9:21 A.M., another premature; 11:10, a defective egg; 11:17, a defective egg; 11:21, a live snake but with one imperfect eye; 11:48, a defective egg; 12:46 P.M., a defective egg; 12:56, a defective egg; 1:00, a defective egg; 1:02, a defective egg; 1:14, a live snake; 2:05, a defective egg. Another bad egg was passed during the night; and early on the morning of August 16 another dead young was born. In connection with these defective broods, it may be noted that they occasionally result in the death of the mother.

C. B. Perkins has observed that 9 out of 10 young rattlers are born with the fetal membrane unruptured. They apparently have little trouble in breaking out, and this they do rather promptly if they are full-term young. They then crawl to a corner of the cage where they coil up and rest.

## YOUNG RATTLESNAKES

### THE EGG TOOTH

Most snakes (and many other reptiles as well) have an egg tooth, a temporary and specialized tooth at the front of the upper jaw. It serves the purpose of aiding the young to cut through the flexible, yet tough, egg sheath that surrounds it. In the ovoviviparous forms, such as the rattlesnakes, the fetal capsules are thinner walled and softer than the eggs from which the oviparous snakes must escape, and the egg tooth is less important. It is inconspicuous and difficult to find, and is to be seen only in embryos or in young just after birth.

In the rattlesnakes, the egg tooth is probably of little value. Hay (1892, p. 386) thought that ovoviviparous snakes might shed the tooth before birth. He found the tooth present in an almost completely developed embryo massasauga (*S. c. catenatus*), but observed it was not pointed forward as in other genera. Allen (1933, p. 14) identified egg teeth in two sets of embryo black-tailed rattlers (*C. m. molossus*), but they were relatively less conspicuous in the set nearest birth. Gloyd (1937, p. 128) observed egg teeth in embryo banded rock rattlers (*C. l. klauberi*), but Kauffeld (1943b, p. 607) could not find them in newly born young of the same subspecies.

Smith, Bellairs, and Miles (1953, p. 265) found that in the massasauga (*S. c. catenatus*) the egg tooth curves upward and probably has no function. In the western diamond (*C. atrox*) and the Mexican west-coast rattler (*C. b. basiliscus*), the egg tooth curves forward, as it does in snakes of the genus *Natrix*. They believe it may be useful for tearing the embryonic covering. Trapido (1939, p. 230) observed that the massasaugas, as they ruptured their fetal membranes, made a series of upward thrusts of the head, a motion that might have brought the egg tooth into play.

I have found the egg tooth in embryos of *C. atrox*, *C. b. basiliscus*, *C. e. enyo*, *C. m. molossus*, *C. v. helleri*, *C. v. lutosus*, and *C. v. nuntius*. It lies medianly in the front of the upper jaw, just back of the recurved and indented edge of the rostral plate. Because of its being so far back, it is difficult to see how it can be of service, unless the snake can thrust forward the premaxillary to which it is attached. In these rattlesnakes, the tooth is so small as to be found with difficulty. In a preserved snake, it can be seen as a slightly yellowish point surrounded by white tissue; and an exploratory needle will show the point to have a hard surface like any tooth. In *Crotalus* it curves from the vertical until the point is directed forward.

#### CONGENITAL DEFECTS

One is impressed with the high proportion of defective young that appear in broods of snakes born or hatched at the San Diego Zoo. This is true of rattlesnakes, among others. It may be presumed that the proportion of defective young and infertile eggs in captive broods exceeds the proportion that occurs under normal conditions in the wild. Here are the records of two broods of red diamond rattlesnakes: First brood—two normal young, one live young but with a defective eye, four born dead, nine eggs (probably infertile); second brood—eight normal young, one alive but with a very small head, one alive but without a left eye, one born dead, nine eggs (probably infertile).

Subsequent to 1931, there were born at the San Diego Zoo 28 rattlesnake broods that contained one or more live young, which shows that fertilization had been effected. There were 274 young or eggs involved. The composition was 70 per cent live young, 12 per cent dead young, and 18 per cent eggs, presumably infertile. Broods containing defective young massasaugas (*S. c. catenatus*) are mentioned by Swanson (1933, p. 37) and by Wright (1940, p. 221; 1941, p. 666).

#### THE FIRST SHEDDING

Young rattlesnakes usually shed their skins for the first time about a week or 10 days after birth. Here are some examples from the records of the San Diego Zoo:

A brood of eleven red diamonds (*C. r. ruber*), born October 16, shed on October 26 and 27; and another brood of three, born August 10, shed on August 21. A brood of three southern Pacifics (*C. v. helleri*), born August 24, shed on September 3; another brood of nine, born August 11, shed between August 19 and 21; and still another brood of three, born September 24, shed on September 30. Six sidewinders (*C. c. laterorepens*) were born on November 4, and all but one shed on November 11. Nine others (*C. c. cerastes*), born on October 15, shed from 8 to 10 days later. A brood of 14 timber rattlers (*C. h. horridus*) was born September 20; the first shedding occurred on October 3, most of the rest on the fifth, and the last by the sixth. Of a brood of four dusky rattlesnakes (*C. t. triseriatus*), two shed on the seventh day, one on the ninth, and the last on the tenth day after birth. In a large brood (26) of the Mexican west-coast rattler (*C. b. basiliscus*), the first shed on the fourth, and the last on the ninth day after birth. More than half shed on the sixth and seventh days. The earliest shedding was observed in a brood of seven Aruba Island rattlesnakes, all of which shed within 16 hours of birth. Shedding within a day of birth was noted in two other broods of this species.

Trapido (1939, p. 230) mentions a brood of timber rattlers that shed 17 to 19 days after birth. Kauffeld (1943b, p. 607) states that a brood of banded rock rattlers (*C. l. klauberi*) shed in 8 to 10 days, and a brood of Arizona twin-spotted rattlers (*C. p. pricei*) in 6 to 10 days. Marcy (1945, p. 169) reported on a brood of Mexican west-coast rattlers (*C. b. basiliscus*), of which the first individual shed on the fourth day, and the rest by the seventh. As to the massasauga (*S. c. catenatus*), Conant (1938, p. 116; 1951, p. 116) mentions a brood that shed within 2 days, and Pope (1944, p. 221) another that shed within 8 days of birth. I think we may conclude that young rattlers usually shed for the first time at an age of from 7 to 10 days.

With their first shedding, young rattlers also shed the rattle with which they are born (the prebutton), for it is thin and flexible and is not greatly different from the skin of which it forms the terminus. This shedding bares the true button, which is not disturbed by subsequent sheddings, but remains at the end of the rattle string until it is eventually lost by breakage. One of the best tests for the age of young rattlers is the presence or absence of the prebutton; if it is still in evidence, the youngster is probably less than 10 days old.

#### YOUNG PER BROOD

Generalities with respect to the numbers of young rattlesnakes in broods are rather unsatisfactory, since there are considerable differences between species. For this reason it is thought best to present in tabular form (table 10:3) such detailed statistics on the subject as have been accumulated within the past thirty years. The data include published figures, San Diego Zoo records, those of my correspondents, and counts of eggs and embryos made on preserved specimens in my laboratory.

Although this table gives some idea of the normal composition of broods, its accuracy is not all that might be desired. Many of the figures, particularly those of the prairie and northern Pacific rattlesnakes, are based on counts of developing eggs, rather than young actually born. It is known from observations on captive snakes, and this seems to be particularly true of those which have been in captivity for some time, that infertile eggs, as well as dead or defective young, are quite prevalent—to such an extent, in fact, that I have estimated that, on the average,

there would be three fewer live young than developing eggs. But no reductions upon this score have been made in the figures contained in the table. Necessarily, were the data restricted to live births, only captive-born broods could be included, for when young rattlers are found with their mothers in the wild, one cannot be sure that they are either a single brood or a complete brood.

If eggs are counted to determine birth rates and sizes of broods, especially during the time when the eggs are in the ovaries rather than in the oviducts, it is necessary to distinguish between eggs and the *corpora lutea*. Also it is essential that there be no conscious selection of adult females with respect to size, since the larger mothers tend to have more young than the smaller. This was shown by counts of developing eggs in the ovaries of two large series of prairie rattlesnakes wherein there was an evident correlation between the size of mother and number of eggs. In these two series, the coefficients of correlation were 0.711 and 0.704 (Klauber, 1936b, p. 19).

From table 10:3 we do note some items of interest. There is a tendency of the larger species to have more numerous broods than the smaller. The subspecies of the tropical rattlesnake (*C. durissus*) and particularly its relative, the Mexican west-coast rattler (*C. b. basiliscus*) are highly prolific.

I am unable to explain the difference in the productivity of the two closely related subspecies of *C. viridis*, the prairie and northern Pacific rattlers, unless it be that the former has compensated for its biennial reproductive schedule by producing larger broods, while the latter, even in the northern areas of the Pacific region, may adhere to an annual schedule, thus producing smaller but more frequent broods. Or it may be that the infant mortality rate is greater in the severer winter climate of the Missouri Basin.

A. M. Jackley had this to say about the fecundity of the prairie rattlesnake:

During the past 25 years I have dissected a great many females to determine their production rate. I found that those bearing young the first time produce from six to eight and in very rare instances only four. I estimate that 75 per cent yield six and 25 per cent eight. The maximum is most interesting. On one occasion I dissected a large female in which there were 23 well developed eggs. The next largest number of sound eggs was 21. The highest numbers of actual embryos were as follows: 2 with 19 and close to 20 with 18. The largest litters found in the field with the mothers were 18 and there were only two of them. Three gave birth to 18 each, within a week after they were captured. Many, though the percentage is low, had 16. Twelve and 14 are common litters for the old snakes. My over-all estimate is an average production rate of 10 biennially.

Some of the published averages and ranges of variation, in the numbers of young per brood or set of developing eggs in the rattlesnakes are the following: Eastern diamondback (*C. adamanteus*) 7 to 18 young, average 9 or 10 (Stickel, 1951, p. 11); western diamondback (*C. atrox*) 4 to 23 young, average 9 (Stickel, 1951, p. 11); sidewinder (*C. cerastes*) 5 to 16 young, average 9 (Stickel, 1951, p. 11); timber rattlesnake (*C. h. horridus*) 5 to 17 young (Lueth, 1941b, p. 21), 5 to 17 young, average 11 (Stickel, 1951, p. 11); red diamond rattlesnake (*C. r. ruber*) 5 to 13 young, average 8 (Stickel, 1951, p. 11); prairie rattlesnake (*C. v. viridis*) 4 to 21 young, average 12 (Smith, 1950, p. 305), 1 to 23 young (Stickel, 1951, p. 11); Great Basin rattlesnake (*C. v. lutosus*) 2 to 9 eggs, average 5.5 (Glissmeyer, 1951, p. 25); northern Pacific rattlesnake (*C. v. oreganus*) 4 to 25 eggs, average 9.9 (Fitch, 1949a, p. 539); eastern massasauga (*S. c. catenatus*), 4 to 13 young (Lueth, 1941b, p. 20), 5 to 14 young, average 8 (Pope, 1944b, p. 221), average 8 to 9 (Smith, 1950, p. 298), 3 to 12 young,

TABLE 10:3  
SIZES OF EGG-SETS AND BROODS

Subspecies	Individuals per set or brood																				
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
<i>C. adamanteus</i> . . . . .	..	..	..	..	..	..	..	1	..	3	3	2	..	..	..	1	1	3	2	1	2
<i>C. atrox</i> . . . . .	..	..	..	2	1	2	8	6	7	..	..	2	..	..	1	1	..	1	..	..	1
<i>C. cerastes cerastes</i> . . . . .	..	..	..	..	..	..	1	1	1	3	1	1	1	..	..	..	..	..	..	..	..
<i>C. cerastes laterorepens</i> . . . . .	..	..	..	..	1	5	5	4	1	4	3	1	1	..	..	2	..	..	..	..	..
<i>C. horridus horridus</i> . . . . .	..	..	..	..	2	2	5	5	6	7	3	7	2	2	..	..	3	..	..	..	..
<i>C. horridus atricaudatus</i> . . . . .	..	..	..	..	..	..	1	..	1	3	2	..	..	..	..	..	..	..	..	..	..
<i>C. lepidus klauberi</i> . . . . .	..	3	4	2	4	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..
<i>C. mitchelli pyrrhus</i> . . . . .	..	..	..	3	3	1	2	1	..	..	..	..	..	..	..	..	..	..	..	..	..
<i>C. mitchelli stephensi</i> . . . . .	..	..	..	..	..	1	..	2	..	3	..	..	..	..	..	..	..	..	..	..	..
<i>C. molossus molossus</i> . . . . .	..	..	3	1	4	1	1	..	..	..	1	..	2	..	..	..	..	..	..	..	..
<i>C. pricei pricei</i> . . . . .	..	..	..	1	1	2	2	..	..	..	..	..	..	..	..	..	..	..	..	..	..
<i>C. ruber ruber</i> . . . . .	..	..	2	1	2	5	3	..	5	1	5	..	2	..	..	1	..	..	..	1	..
<i>C. ruber lucasensis</i> . . . . .	..	..	4	2	3	2	1	1	..	..	1	1	..	..	..	..	..	..	..	..	..
<i>C. scutulatus scutulatus</i> . . . . .	..	..	..	..	3	3	3	2	5	2	2	..	1	..	..	..	..	..	..	..	..
<i>C. triseriatus triseriatus</i> . . . . .	..	1	..	3	1	1	..	..	1	..	..	1	..	..	..	..	..	..	..	..	..
<i>C. unicolor</i> . . . . .	..	..	..	..	..	1	1	..	2	1	..	..	..	1	..	..	..	..	..	..	..
<i>C. viridis viridis</i> . . . . .	..	..	..	3	8	8	13	29	39	40	24	35	24	19	23	15	15	7	2	2	1
<i>C. viridis caliginis</i> . . . . .	1	2	3	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
<i>C. viridis helleri</i> . . . . .	..	1	1	..	1	..	2	..	2	1	1	1	1	..	..	1	..	..	..	..	..
<i>C. viridis lutosus</i> . . . . .	..	..	2	1	4	9	5	4	3	1	3	1	5	..	..	..	..	..	..	..	..
<i>C. viridis nuntius</i> . . . . .	..	..	1	1	2	..	1	1	2	2	..	..	..	..	..	..	..	..	..	..	..
<i>C. viridis oreganus</i> . . . . .	1	2	12	14	10	4	8	3	7	6	4	3	4	1	..	..	..	..	..	..	..
<i>S. catenatus catenatus</i> . . . . .	..	1	1	4	7	3	6	13	6	1	2	3	5	1	..	..	..	..	1	..	..
<i>S. miliarius barboursi</i> . . . . .	..	2	..	2	2	1	1	3	1	..	1	..	1	..	..	..	..	1	..	..	..

For statistics supplemental to this table see p. 702.

average 7 (Stickel, 1951, p. 11); southeastern pigmy rattlesnake (*S. m. barbouri*) average 8 to 9 (Allen and Neill, 1950b, p. 10); (*S. miliarius*) 5 to 18 young, average 8 to 9 (Stickel, 1951, p. 11). Some of these figures may have been derived from my own previously published table (Klauber, 1936b, p. 22).

Two very large broods reported in the literature have not been included in the table. Bridges (1944, p. 125; Duncan, 1945, p. 171) mentions a medium-sized western diamond rattler (*C. atrox*) that gave birth to 46 young—26 alive and 20 dead. The magazine *St. Louis Zoo* (vol. 11, no. 4, p. 3, 1940) reported a diamondback that gave birth to 52. There may have been confusion with the prolific Mexican west-coast rattler (*C. b. basiliscus*).

On the fantastic side, Carver (1779, p. 485) claimed to have killed a mother timber rattler with 70 young; he had seen her swallow them for protection. Beltrami (1828, vol. 2, p. 162) was told by a man of "unimpeachable veracity" that he had killed a mother rattler that contained 140 young, several of which, in turn, contained other young ones. Spoofing the tenderfoot was no doubt an ancient practice even then.

In summary, it may be said that our commonest and most important species of rattlesnakes found in the United States probably average 8 to 10 young per brood.

Data supplemental to table 10:3:

a. Subspecies of which less than five records are available (in the range 1 to 21 young):

- C. basiliscus basiliscus* 14, 20
- C. cerastes cercobombus* 10
- C. durissus durissus* 12, 18
- C. durissus terrificus* 10, 12, 16, 19
- C. enyo enyo* 6, 9
- C. exsul* 3
- C. intermedius omiltemanus* 4
- C. lepidus morulus* 3, 4, 8
- C. mitchelli mitchelli* 3, 4, 4, 5
- C. mitchelli muertensis* 1, 3
- C. molossus nigrescens* 2, 4
- C. polystictus* 3, 20
- C. tigris* 4, 5
- C. tortugensis* 5, 6
- C. triseriatus aquilus* 4
- C. viridis abyssus* 6, 13
- C. viridis cerberus* 6, 6, 9
- C. viridis decolor* 7
- C. willardi willardi* 6, 9
- C. willardi silus* 2
- S. catenatus tergeminus* 3, 4, 9, 9
- S. miliarius miliarius* 3, 9
- S. miliarius streckeri* 4, 6, 6, 7
- S. ravus* 8, 9

b. Records above 21 eggs or young:

- C. atrox*, 22, 23, 24
- C. basiliscus basiliscus* 26, 26, 28, 29, 30, 30, 31, 41, 47, 49, 60
- C. durissus durissus* 47
- C. durissus totonacus* 37
- C. horridus horridus* 22, 30

## VARIATIONS IN SIZE OF YOUNG

The smaller kinds of rattlesnakes have proportionately larger young than the larger species. In the smallest species the young, when born, measure 30 per cent or more of the ultimate size reached by the adult males, whereas in the largest species the young at birth measure only about 18 to 20 per cent of the full-grown males. For example, an adult male Carolina pigmy rattler reaches a length of about 530 mm. (21 in.) and the young at birth are about 160 mm. (6¼ in.) or 30 per cent of ultimate length. On the other hand, a large male red diamond rattler may reach 1,400 mm. (55 in.); the young at birth average 300 mm. (11¾ in.) or only 21.4 per cent of ultimate size. Further data giving the lengths of most species of rattlesnakes at birth and the ultimate adult size will be found in table 4:1. An approximate generic curve expressing the relationship between the average size at birth ( $B$ ) and the size of a large male ( $L$ ), both in millimeters, is given by the following equation:  $B = 37.0 + 0.263L - 0.00000521L^2$ . Sexual dimorphism in size at birth is almost negligible; the males average about one per cent longer than the females (Klauber, 1937, p. 12).

As has been pointed out, within each species or subspecies of rattlesnake the larger mothers tend to have more young than the smaller. It has been stated by some, that when the broods are smaller the individuals comprising them are larger, so that a sacrifice in numbers gives the youngsters a better start in life. I failed to find this latter correlation in a series of broods of the prairie rattlesnake from Montana (Klauber, 1937, p. 8), but additional studies of larger series might validate the hypothesis.

A. M. Jackley was of the opinion that there may be annual differences in the size of the young, caused by weather differences. He wrote:

The rattlers in this vicinity give birth to their young within a period of four weeks, beginning about August 15th. But in 1942 the young were born on an average of about 10 days later than usual, and in 1943 as much as two weeks later, and the young seemed stunted. In the spring of 1942, because of the weather, the snakes were not able to leave their dens until early in June, and, in 1943, many were delayed until July.

There is a considerable dispersion in the size at birth of the youngsters comprising a single brood. I investigated the extent of this variation in a number of broods (Klauber, 1937, p. 7) and found that, in broods comprising not less than eight young, and omitting any broods measured more than a week after birth, the coefficient of variation averaged about 3½ per cent. Additional calculations indicated that the coefficients of most natural broods are below 4 per cent. The size dispersions of the young snakes are found to follow the normal probability curve, except that stunted specimens, or runts, are more common than those that are unusually large.

To visualize what this variation means in a typical brood, assume a brood of red diamond rattlers averaging 12 inches in length. Then about half of the youngsters will fall between 11.7 and 12.3 inches; and 90 per cent will be no shorter than 11.2 nor longer than 12.8 inches. This gives an idea of the consistency implied in a coefficient of variation of 4 per cent.

As already mentioned, broods of young snakes born (or hatched from eggs) in captivity often contain defective or deformed individuals—snakes with small heads,

without eyes, with a fused loop of the body, etc. Others, although well formed, are obviously stunted. Many of these defects are lethal, so that even if the young are born alive they cannot long survive. But although this elimination of defectives tends to decrease variations within a brood, the coefficient of variation in length, in a group of unrelated youngsters, is usually higher than in a brood, since parental heterogeneity, which may be either genetic, environmental, or both, becomes effective. Thus, in groups of young not restricted to a single brood, the coefficient of variation is likely to be about 5 per cent; and within a short time after birth the variations in length become still greater because of the variable fortunes of the individuals in the securing of food. Hence, by the time the young snakes enter their first hibernation, the coefficient of variation of the young-of-the-year is likely to reach, or somewhat exceed, 8 per cent.

#### MATERNAL PROTECTION AND ASSOCIATION

It is generally believed that young rattlesnakes remain with their mother for only a few hours after birth, or a day or so at most. Their propinquity, such as it is, does not result from any maternal solicitude; rather it is only because the refuge sought by the mother is also used as a hiding place by the young. Thus, when a mother is found with her brood it may be taken as an indication that their birth was of recent occurrence. Of course, the mere presence of young with an old rattler is not always proof of a maternal relationship. However, if the young still have their prebuttons, a proof that they have not shed for the first time, they are probably less than 10 days old, and may indeed be a brood. This matter of the association of young with their mother would not be complete without mention of the widespread belief that mother rattlesnakes swallow their young for protection when danger threatens. This myth has been discussed at some length elsewhere (p. 1276).

There have been several published accounts of young found with their mothers. Audubon, in his journal (1906, p. 146), tells of digging out a rattler (presumably a western diamond) from a hole under mesquite and cactus in Arizona. At a depth of two feet a mother rattler was found with nine young. Gloyd (1937, p. 121) came upon a western diamond (*C. atrox*) female with her newly born brood of eight. When disturbed, they took refuge in rocks behind the mother. This was on the morning of July 31, 1930, near the mouth of Carr Canyon, Huachuca Mountains, Arizona.

Dunkle and Smith (1937, p. 13) found several Mexican black-tailed rattlers (*C. m. nigrescens*) in July with their broods under rocks and a ledge along a canyon rim—that is, they were assumed to be mothers and broods, although adult males were also present. P. Anderson (1942, p. 217) found a female timber rattler (*C. h. horridus*) with four young in Jackson County, Missouri, September 8, 1941.

Some of the observations of mothers and young made by my correspondents are as follows:

The mother instinct has never been noted in rattlesnakes. The mother saves herself if she can, leaving the young to shift for themselves. There is a current story, repeated by the mountain people hereabouts, to the effect that when you approach a mother rattler, she will swallow her young, and when danger has passed, she will permit them to crawl from her mouth. This I have never seen, or thought to be true. *John H. Stanley, U. S Forest Service, Andrews, N. C.*

Rattlers pay but small attention to their young. They are mostly on their own after being born. *Riley R. Osborn, Game Warden, Torrey, Utah.*



My father, while riding in the Cassia East District of the Minidoka National Forest, came upon a large rattler. It acted queerly and went under a rock. Because of its peculiar actions he got a pole and pried the rock over. He found the old snake and twelve young about 10 inches long. *Merlin R. Stock, U. S. Forest Service, Twin Falls, Idaho.*



I ran across a rattlesnake, a fair-sized one about three feet long, lying coiled up on a flat rock. The rock was about two inches thick. I killed the snake and was about to leave when I noticed two small ones under the edge of the slab. I turned the rock over and found 18 in all. *Eddie Buchta, U. S. Fish and Wildlife Service, Moneta, Wyo.*



While it is possible that a mother rattler protects her young for a week or so, yet it seems more likely she remains in one place only to recuperate after their birth. At any rate, when she comes out of her retreat and assumes a resting position, the little fellows like to coil on top of her, or closely against her sides. I captured two such females whose litters were shedding, thus indicating how long they had stayed with their mothers, for young rattlers shed their skins for the first time from 7 to 10 days after birth. But soon the mother must go hunting for food and so they scatter.

Here is one such occurrence: Ten little ones, probably three days old, were bunched by the side of a hole about two inches in diameter. I watched them for some time, hoping the mother would come out and join them. Finally, concluding that she would not, I drew them away from the hole with a quick jerk of my rake. Almost instantly the mother came halfway out of the hole and made a quick lunge for the rake. *A. M. Jackley, Pierre, S. Dak.*

Henry Shelton told me that when he overturned a rock under which there was a southern Pacific rattlesnake and her brood of 11 young, the mother seemed to try to protect the young, and did not attempt to escape until all were killed.

There will be noted in these accounts some discrepancies as to the length of time the mother remains with her young, and the degree of protection she exercises. As I stated initially, there is no final evidence that young rattlers stay with their mothers for more than a day or so at most; if they are found together there is no proof that the young rattlers are more than a few days old or that their propinquity is caused by other than the use of a common refuge. The sizes of young rattlesnakes are consistently underestimated by observers, just as adult lengths are exaggerated. One correspondent mentioned snakes as short as two and one-half to three inches, and another thought the young must have been with the mother for some time as they had attained a length of eight inches. But, as a matter of fact, the young of even the smallest species of rattlesnakes are about six inches long at birth, and such common forms as the subspecies of the western rattlesnake are about 10 inches, and of the diamondbacks 12 inches or more.

Only the finding of a mother rattler with a brood, the members of which had not shed for the first time, would prove that the young had remained with the mother upward of a week or so, which is the average interval between birth and the first shedding. But unfortunately, even then, there would be no proof that the young were actually hers.

In captivity mother rattlesnakes evince no solicitude for their recently born young. True, the young often lie close to or even on the mother, but this is only because of the natural gregariousness of snakes in or out of captivity; they seem

just as likely to do this with some other rattler, not the parent. Bevan (1927, p. 100) stated that the mothers exercise no maternal protection. He had seen them give birth to young, and then leave without evidence of the slightest interest in them. Matteson (1899, p. 667) tried to excite a mother rattler (*C. v. viridis*) by tantalizing her young, but she seemed to have no regard for them.

Some presumptions in a fantastic vein have been voiced by John Burroughs (1908, p. 18), who believed that young rattlers might be taken into the mother's stomach so that they could be fed; and the account by Meek (1946, pp. 24, 250) of how young diamondbacks are not weaned until they reach a length of a foot, at which time the mother leads them along a trail, where she leaves them to fend for themselves, at suitably spaced intervals. Crites (1952, p. 62) found a mother rattler crooning (by rattling mildly) to her newly born young.

#### DISPOSITIONS OF YOUNG RATTLESNAKES

Young rattlers are more pugnacious than adults—more easily aroused and ready to defend themselves. This, however, is characteristic of many kinds of snakes—of king snakes and gopher snakes, for example, of which the young are more ready to bite than the adults. Newly born rattlers, although they can make no rattling sound, nevertheless vibrate their tails just as do the adults, and take on a fine fighting pose.<sup>5</sup> My correspondents have made the following statements about the actions and dispositions of young rattlers:

I have observed very young prairie rattlesnakes on several occasions, always in late summer. The young were pugnacious, striking wildly and repeatedly, and made no attempt to escape. I have never observed the parent with the young. *W. E. Beed, Fish and Wildlife Service, Waupun, Wis.*



The young of the Great Basin rattler were found to be very vicious and ready to strike without much provocation; however, as the snakes grew older, they seemed to lose their aggressiveness. *Russell K. Grater, National Park Service, Estes Park, Colo.*



If a mother rattler be killed, young rattlers about to be born will strike instinctively when removed from the egg sac. *A. C. Mackie, Vernon, British Columbia.*



The smaller rattlers seem to be the most ready to strike. *Floyd C. Black, U. S. Fish and Wildlife Service, Challis, Idaho.*



At a locality in the Wylie Mountains, 16 miles southeast of Van Horn, Culberson County, Texas, elevation 4,100 feet, on July 30 or 31, 1940, my students and I encountered a large western diamond rattler (*C. atrox*) in a cavity under a rock, the entrance to which looked as if it might once have been occupied by some mammal. We were setting mouse traps and looking for suitable sites, when the rattler buzzed, causing us some consternation. One of the boys shot into the cavity, killing the snake. We dragged it out, cut it open and found 12 unborn snakes in the reproductive tract. Upon removing the fetal membranes, the young snakes were found to be very much alive, aggressive, and ready to strike at any object that threatened them. As I recall, they were able to exude a drop or two of venom, but I cannot vouch for this as I made no record at the time. *W. B. Davis, Texas A. & M. College, College Station, Tex.*

There is no reason to doubt Dr. Davis' observation on the venom, for the young snakes do have venom and are dangerous at birth, although much less so than

<sup>5</sup> If they are threatened, young cobras, immediately after birth, will expand their hoods in a characteristic defensive posture (Benchley, 1944, p. 1).

adults because, as discussed elsewhere (p. 813), of their shorter fangs and smaller quantity of venom. Several young sidewinders, under observation in a glass jar, seemed to be excited by the movements of their fellows, and struck each other as they moved about. No adverse results were subsequently noted. Young rattlesnakes of nearly all species are more brightly and clearly marked than the adults, with an accentuated contrast between blotches and ground color. There are other ontogenetic changes in pattern and color, as mentioned elsewhere (p. 224).

#### ACTIVITIES OF YOUNG RATTLESNAKES

Young rattlers remain with their mothers only to the extent that mother and offspring seek the same refuge or place of concealment. The individuals of the brood soon scatter in search of food; under no circumstances could the mother aid them in this search, for each must obtain its own live prey. Nor do the young rattlers of a brood stay together as supposed by Ingersoll (1883a, p. 35; 1884b, p. 90), for they are competitors for a limited food supply. It seems almost superfluous to point out that snakes swallow their prey whole; and rattlers, of course, are no exceptions. Snakes have no mechanism, either in their teeth or otherwise, for dismembering prey. Thus, stories of mother rattlers sharing food with the young are quite contrary to fact.

In the discussion of birth rate, I have already pointed out that there is a considerable reduction in the proportion of a population constituted by the young-of-the-year, during the time from their births in the fall, to the end of their first hibernation in the spring. Lack of food, freezing, and vulnerability to predators take their toll. The food problem is a serious one for the little rattlesnakes, for they are limited to lizards and very small rodents. Although we have observed at the Zoo that young can survive for some months after birth without food, because they are fat with absorbed egg yolk when born, the growth and vigor of those that have fed, compared with those that have not, show how serious the lack of food must be to those in the wild that are unsuccessful in securing any prey.

I have experimented in a limited way to determine whether the juveniles can survive the first winter without food. What tests I have made indicate that they cannot. At least I can say positively that many would not, and I seriously question whether any could. On the other hand, I am confident that one field mouse would be sufficient to carry one through its first winter. *A. M. Jackley, Pierre, S. Dak.*

Wright (1944, p. 667) attributed the high mortality among young massasaugas (*S. c. catenatus*) to their inability to secure food.

The second serious cause of mortality among the young is that of freezing during the first winter, particularly because many of the young fail to reach havens previously tested and found safe by their forebears. Thus they may take refuge in holes or crevices that are not below the frost line, or that are subject to fatal drafts, and never awaken to see the spring.

Finally there is predation, for the young snakes are inexperienced, careless of concealment when searching for food, and are preyed upon by creatures that could not successfully cope with their more dangerous parents. Fitch and Glading (1947, p. 122) and Fitch (1949a, p. 539) believe predation to be an important cause of high mortality among the infant rattlers.

That there may be species differences in the conduct of the young, is indicated by studies made in San Diego County. Here there seems to be no great difference in the adult populations of the southern Pacific (*C. v. helleri*) and red diamond (*C. r. ruber*), but the juveniles of the former are found in about ten times greater numbers than the latter. The young reds seem instinctively to take care of themselves better by remaining hidden (Klauber, 1931b, p. 20).

Behr (1888, p. 95) believed that young rattlers are more nocturnal than the adults. This is certainly not true of the southern Pacific rattlesnake, although it might explain the comparative scarcity of young red diamonds. Fitch (1949a, p. 522) found that young northern Pacific rattlers (*C. v. oreganus*) emerged earlier in the evening than the adults.

